RESOURCE PARTITIONING BETWEEN BREEDING COMMON (*URIA AALGE*)

AND THICK-BILLED MURRES (*URIA LOMVIA*)

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RESOURCE PARTITIONING BETWEEN BREEDING COMMON (*URIA AALGE*) AND THICK-BILLED MURRES (*URIA LOMVIA*)

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ABSTRACT

In seabirds, food availability is a driver of ecological and evolutionary processes. Here we examine how changes in food availability and energy demands affect both inter-specific resource partitioning and the genetic diversity within a species.

We examined the effects of interannual fluctuations in food availability and predictable seasonal increases in energy demands on prey partitioning between breeding common (*Uria aalge*) and thick-billed (*U. lomvia*) murres. We observed strong spatial, temporal and dietary differences in the use of prey resources between the species. We found that partitioning increased as food availability declined and as energy demands increased during chick-rearing. We conclude that murres can buffer negative effects of warming and increased energy demands by reducing inter-specific competition for limited food resources.

We also investigated the effects of contrasting foraging conditions and population trajectories on the genetic structure of common murres. We found that birds breeding on an increasing food-rich colony had higher genetic diversity than conspecifics breeding on a declining food-poor colony. This may be indicative of changes in a relative strength of purifying selection operating on increasing versus declining colonies. We conclude that foraging conditions might be driving the pattern of the genetic diversity in the Pacific common murre population.

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INTRODUCTION

The theory of ecological niche separation predicts that sympatric species cannot completely overlap in all aspects of their ecology if they compete for any resources (Pianka, 1969, Lack, 1946). However, the extent of inter-specific resource partitioning is expected to vary in response to fluctuations in the environment (Goldberg & Barton, 1992, Pianka, 1969, Schoener, 1974). Species can partition food resources in space, time, and diet selection (Wilson, 2010). In the North Pacific, fluctuations in prey availability are typically determined by changes in the oceanographic conditions (such as variations in water temperature or winter ice extent and timing of retreat) that might affect food resources available to different species of seabirds breeding at the same colony, which would affect the extent of their food resource partitioning (Forero, Bortolotti, Hobson *et al.*, 2004). In long lived species, such as seabirds, it is well known that food resources are a key driver of population dynamics (Navarro, Forero, Gonzalez-Solis *et al.*, 2009, Weimerskirch, Jouventin & Stahl, 1986). However, few studies have addressed how environmental changes that affect food availability might affect resource partitioning. Dramatic increases in parental energy demands associated with chick-rearing might also affect the foraging responses in seabirds (Ito, Takahashi, Kokubun *et al.*, 2010, Wilson, 2010, Deagle, Gales & Hindell, 2008, Monaghan, Uttley, Burns *et al.*, 1989, Montevecchi, Birt-Friesen & Cairns, 1992). Thus, we might be able to predict and detect differences in resource partitioning in response to environmental changes and a predictable increase of energy demands between the incubation and chick-rearing stages of reproduction.

In this study we combined several techniques to investigate resource partitioning between common (*Uria aalge*) and thick-billed (*Uria lomvia*) murres breeding at the same colony. Murres are abundant colonial seabirds that often share nesting and foraging habitats and both species are sensitive to fluctuations in the prey abundance. In chapter 1 and 2, we used the adrenal hormone corticosterone (CORT) as an indirect measure of prey availability, as previous studies have shown CORT to be an effective proxy for relative changes in prey availability in seabirds (Wingfield, Vleck & Moore, 1992, Kitaysky, Piatt, Hatch *et al.*, 2010, Kitaysky, Piatt & Wingfield, 2007, Kitaysky, Wingfield & Piatt, 1999, Dorresteijn, Kitaysky, Barger *et al.*, 2012, Satterthwaite *et al.*, 2012, Doody, Wilhelm, McKay *et al.*, 2008). We also examined stable carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of red blood cells to compare the diets of adult murres (Cherel, Le Corre, Jaquemet *et al.*, 2008, Inger & Bearhop, 2008, Thompson, Lilliendahl, Solmundsson *et al.*, 1999). This approach detects changes in diet or foraging habitat selection depending on the variability in prey stable isotope (SI) ratios, and is widely applied in studies of seabird foraging ecology (Thompson *et al.*, 1999, Navarro *et al.*, 2009). In chapter 2, we attached time-temperature-depth recorders (TDR) to the ventral surface of chick-rearing murres to compare foraging patterns (diving frequency and depth, water temperatures, and flight distance between breeding colony and foraging grounds) between the species. Previous studies have shown that TDRs can detect differences in foraging ecology in seabird species (Ito *et al.*, 2010, Wilson, 2010).

In Chapter 3, we investigated the genetic structure of common murres breeding on three Bering Sea colonies with contrasting foraging conditions and population

trajectories. The primary goal of this study was to examine whether a declining breeding colony has less genetic diversity than a colony that is increasing or stable in number. To evaluate the genetic diversity, we sequenced the mtDNA gene NADH dehydrogenase subunit 2 (ND2) in a large number of individuals breeding on St. Paul (declining colony), St. George (stable colony) and Bogoslof (increasing colony) (Byrd, Schmutz & Renner, 2008, Klostermann, Scopel & Drummond, 2011, Renner & Williams, 2005). In seabirds, prey availability is a dominant factor driving population dynamics. Considering the vast differences in oceanographic conditions among these three breeding colonies, foraging conditions are likely to be the main driver of the observed contrasting numerical trajectories (Byrd *et al.*, 2008). Pacific common murres are also known to experience decadal mass die-offs (250,000 birds or 9% of the total population) due to starvation on the wintering grounds (Drovetski, Kitaysky, Mode *et al.*, 2012, Piatt & VanPelt, 1997). In a comparative study between breeding (live) birds and birds that perished during a die-off (dead), it was determined that individuals with any mutation in the ND2 gene died in disproportionate numbers compared to carriers of a dominant haplotype (Drovetski *et al.*, 2012). Therefore, food shortages in the Pacific common murre might be a common factor causing die-offs of individuals on the wintering grounds and declines at breeding colonies.

CHAPTER 1

ISOTOPIC SEGREGATION BETWEEN SYMPATRIC SEABIRD SPECIES INCREASES WITH NUTRITIONAL STRESS[1]

ABSTRACT

Dietary segregation is essential for the coexistence of closely related species of animals. However, little is known about how changes in availability of food resources might affect trophic interactions of wild animals breeding in sympatry. Here we examined how interannual variations in relative food availability (as reflected in blood levels of stress hormone corticosterone, CORT) affect food partitioning (assessed via a comparison of stable isotope $\delta^{15}N$ and $\delta^{13}C$ ratios of blood) between the common murre (*Uria aalge*) and thick-billed murre (*U. lomvia*) breeding on a single colony in the Bering Sea. During a six-year study, CORT varied among years but not between species, whereas stable isotope ratios varied among years and between species. Isotopic distance between species increased with increasing CORT. These results indicate that, when food was not limiting, both species relied on similar food resources. As foraging conditions deteriorated, murres diverged in their diets. We conclude that the degree of dietary segregation between *Uria* spp. varies with changes in availability of food and is greatest during food shortages.

[1]Barger, C. P., & A. S. Kitaysky. 2012. Isotopic segregation between sympatric seabird species increases with nutritional stress. Biology Letters 8: 442-445.

Introduction

The ecological theory of segregation predicts that multiple species competing for a single resource cannot persist indefinitely [1] and diet segregation, either through habitat selection or resource partitioning, is essential for coexistence of morphologically similar species [2]. In seabirds, food partitioning has been proposed as one of the major mechanisms responsible for the coexistence of several taxa at a single colony [3, 4]. Interannual fluctuations in prey available to seabirds are usually driven by changes in oceanography and might affect the magnitude of the diet segregation needed for two species to coexist. An overlap in diets might reflect a superabundance of food, while diet segregation might be needed to alleviate competition for limited food resources; however, empirical data are limited [5].

Previous studies have shown that blood concentrations of the adrenal hormone corticosterone (main avian glucocorticosteroid, CORT) is an effective proxy for monitoring relative prey availability in seabirds [6, 7]. Body tissue signatures of stable isotopes (SI) $\delta^{15}N$ and $\delta^{13}C$ ratios have been used to profile trophic niches of individual seabirds [8]. While $\delta^{15}N$ reflects the trophic level of prey consumed, $\delta^{13}C$ indicates the spatial origin of food resources [8]. Here we combine these techniques to determine how diet segregation between two closely related species of seabirds varies with interannual changes in prey availability and oceanographic conditions. Common and thick-billed murres are colonial seabirds that often breed sympatrically in arctic and subarctic regions. Previous studies assessed murre diets during reproduction through observations of food delivered to chicks, but adult diets are relatively unstudied (but see [9]). The segregation

theory predicts that such species would always segregate their foraging when breeding in sympatry, however, the empirical evidence is equivocal: murres have shown strong dietary differences in some instances [10] and utilization of similar prey in others [11]. Causal factors contributing to these variations in food partitioning are currently unknown, but changes in food availability have been suggested as a potentially important mechanism [12]. Diet segregation between the species could reflect changes in availability of food such that when food resources are abundant murres overlap in their diets [10], but when food becomes limited foraging niches become segregated [11]. Here we test the prediction that greater food partitioning (as reflected in more distant SI ratios) will be observed in years with low food availability, as reflected in elevated CORT levels.

Methods

Murre samples were collected on Bogoslof Island (53°55′38″N 168°02′04″W) in the southeastern Bering Sea during July 15th - August 1st in 1999, 2000, 2004-05, and 2008-09.
Productivity of the southeastern Bering Sea and Gulf of Alaska ecosystems is affected by interannual changes in oceanographic conditions such that colder conditions are usually associated with higher abundance of zooplankton [e.g. 13, and references therein], which in turn might increase availability of prey to murres [14]. We used the annual mean May sea-surface temperature (SST) in the southeastern Bering Sea (available at www.beringclimate.noaa.gov) as a proxy for changes in environmental conditions.

We focused on incubating adults to avoid the potential effects of chick requirements on parental foraging. Birds were captured at mixed colonies of murres with noose poles and a blood sample was collected from the brachial vein within three minutes to reflect baseline CORT levels

[6, 15]. Red blood cells (RBC) and plasma were separated by centrifugation and stored at -20 °C until further analysis. Plasma concentrations of CORT were determined as previously described [6, 15]. Inter and intraassay variability coefficients were less than 6% and 2% respectively.

SI ($\delta^{13}C$, $\delta^{15}N$) were analyzed from RBC. The use of RBC is important for two reasons; (1) it reduces the possibility of interference from lipids (most are removed with plasma); (2) RBC are continuously replaced and provide a proxy of recent diet composition [16]. To provide information on the isotopic scope of prey, we report SI ratios of the main potential prey species [9] collected in the proximity of the colony in 2009. SI in RBC and lean whole body tissue of prey were determined as previously described [17]. Replicate measures of internal laboratory standards indicated measurement errors to be ± 0.16‰ $\delta^{15}N$ and ± 0.13‰ $\delta^{13}C$ in RBC, and ± 0.12‰ $\delta^{15}N$ and ± 0.09‰ $\delta^{13}C$ in prey.

All statistical analyses were performed with STATISTICA v.10. We used three separate general linear models (GLMs) to determine differences in baseline CORT, $\delta^{13}C$, and $\delta^{15}N$ between years and species. CORT data were log-transformed to meet assumptions for parametric statistical comparisons. To examine how changes in diet segregation correspond with changes in CORT and SST, we conducted correlation analyses between calculated isotopic distance (based on Euclidean distances of mean $\delta^{13}C$ and $\delta^{15}N$ signatures between species for each year, annual mean CORT for each species, and SST) (Appendix 1.1 and 1.2). We also examined whether the species-specific variance in SI increased during the years with high CORT using Pearson correlation analyses.

Results

Baseline CORT levels were similar between species ($F_{1,296} = 1.33$, $p = 0.250$) but varied among years ($F_{5,296} = 6.44$, $p < 0.001$); interannual changes in CORT were parallel between species ($F_{5,296} = 1.41$, $p = 0.222$; Figure 1.1). In contrast, SI ratios were different

between species ($\delta^{13}C$: $F_{1,148} = 101.3$, $p < 0.001$; $\delta^{15}N$: $F_{1,148} = 5.26$, $p = 0.023$; Figure 1.1) and years ($\delta^{13}C$: $F_{5,148} = 16.7$, $p < 0.001$; $\delta^{15}N$: $F_{5,148} = 26.73$, $p < 0.001$; Figure 1.1); interannual changes were not in parallel between species ($\delta^{13}C$: $F_{5,148} = 8.3$, $p < 0.001$; $\delta^{15}N$: $F_{5,148} = 3.25$, $p = 0.008$). Interannual changes in $\delta^{13}C$ and $\delta^{15}N$ variance did not correlate with changes in mean CORT in common and thick-billed murres (r-values < 0.63, n=6, associated p-values > 0.176). Isotopic distances between species were positively correlated with CORT levels of common ($n = 6$, $r = 0.83$, $p = 0.043$) and thick-billed ($n = 6$, $r = 0.86$, $p = 0.030$) murres (Figure 1.2a). Isotopic distances between species were positively correlated with SST ($n = 6$, $r = 0.898$, $p = 0.015$; Fig. 1.2b).

Discussion

This study provides novel insights concerning the importance of changes in food availability on diet segregation between closely related species that breed in sympatry. Common and thick-billed murres breeding on Bogoslof I. share breeding habitat and are similar in reproductive phenology and colony attendance patterns: one would expect to find large differences in their foraging ecology. This study shows that when food was limited (elevated CORT) murres displayed niche partitioning (increased isotopic distance) by feeding on different prey and/or utilizing alternate foraging habitats. However, we found that diet segregation was not static, as interspecific differences in isotopic signatures were negligible when food was abundant and only increased when nutritional stress became elevated (Fig. 1.2a). The divergence into different foraging niches may allow murres to avoid interspecific competition for limited food resources and meet the demands of reproduction during sub-optimal conditions.

Previous studies have shown that seabirds respond to food limitations through an increase in CORT secretion [15]. We found that CORT levels changed in parallel in both murre species during the six breeding seasons indicating that they were similarly affected by interannual environmental changes. The similarity of the relationships between isotopic distance and CORT or SST, suggest that food limitations were induced by the interannual change in oceanographic conditions. During food-limited "warm" years with higher levels of CORT, common (but not thick-billed) murres generally had higher $\delta^{15}N$ ratios compared to food-rich "cold" years. This suggests that during food-limited conditions common murres were utilizing higher trophic level prey species (e.g. smelt and myctophids, according to prey SI in the vicinity of the colony) than thick-billed murres (Fig. 1.1). This is in accordance with previous direct observations of the diet composition in these species [10, 11].

The isotopic distance between species was also driven by fluctuations in the common murre $\delta^{13}C$ ratios during years with elevated nutritional stress (Fig. 1.1). Interestingly, we found that the $\delta^{13}C$ ratios in thick-billed murres were generally low and remarkably constant across years, while common murres had larger variability between the years and their $\delta^{13}C$ ratios were always higher. Perhaps diet segregation in these two species was largely due to changes in common murre foraging habitat selection. The higher $\delta^{13}C$ ratios of common murres in food-limited years suggests that this species could have foraged on prey located in the shelf region of the Aleutian Archipelago, which is influenced by inflow of waters from the central Gulf of Alaska and characterized by relatively high $\delta^{13}C$ [18]. In contrast, thick-billed murres seemed to be continuously

feeding in oceanic waters surrounding Bogoslof Island on prey relatively low in $\delta^{13}C$ [19].

Examining food limitations in conjunction with the degree of isotopic segregation between two potentially competing species provides a better understanding of the changes that occur in their foraging ecology in response to environmental variability (Fig. 1.2). Results of this study suggest that interspecific diet partitioning is dynamic and might be indicative of the negative effects of warming environmental conditions on food resources available to seabirds breeding in the ocean basin regions of the Bering Sea (Fig. 1.2). Our approach to quantifying interspecific trophic interactions highlights the potential impact of warming climate on dietary niche overlap between species, which has implications for other bird species that share resources. Despite the apparent utility of this study, there are shortcomings that must be addressed in future research. During years with small interspecific isotopic distance, murres could have potentially foraged on different prey with similar SI ratios. Although the very low SI ratios of the age-0 pollock (Fig. 1.1) make them a likely main prey of both murres during some years (i.e. 2005), we only obtained SI of prey collected in 2009 and could not account for the temporal variability of SI of prey in other years. Whether diet segregation varies among life-history stages even during favorable foraging conditions also remains to be examined.

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Literature Cited

1 Lack, D. 1946 Competition for food by birds of prey. *Journal of Animal Ecology*. **15**, 123-129.
2 Pianka, E. R. 1969 Sympatry of desert lizards (Ctenotus) in western Australia. *Ecology*. **50**, 1012-1030.
3 Weimerskirch, H., Jouventin, P., Stahl, J. C. 1986 Comparative ecology of the 6 albatross species breeding on the crozet islands. *Ibis*. **128**, 195-213.
4 Navarro, J., Forero, M. G., Gonzalez-Solis, J., Igual, J. M., Becares, J., Hobson, K. A. 2009 Foraging segregation between two closely related shearwaters breeding in sympatry. *Biology Letters*. **5**, 545-548. (doi:10.1098/rsbl.2009.0150)
5 Forero, M. G., Bortolotti, G. R., Hobson, K. A., Donazar, J. A., Bertelloti, M., Blanco, G. 2004 High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. *Journal of Animal Ecology*. **73**, 789-801. (doi:10.1111/j.0021-8790.2004.00852.x)
6 Kitaysky, A. S., Piatt, J. F., Wingfield, J. C. 2007 Stress hormones link food availability and population processes in seabirds. *Marine Ecology-Progress Series*. **352**, 245-258. (doi:10.3354/meps07074)
7 Kitaysky, A. S., Piatt, J. F., Hatch, S. A., Kitaiskaia, E. V., Benowitz-Fredericks, Z. M., Shultz, M. T., Wingfield, J. C. 2010 Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Functional Ecology*. **24**, 625-637. (doi:10.1111/j.1365-2435.2009.01679.x)
8 Thompson, D. R., Lilliendahl, K., Solmundsson, J., Furness, R. W., Waldron, S., Phillips, R. A. 1999 Trophic relationships among six species of Icelandic seabirds as determined through stable isotope analysis. *Condor*. **101**, 898-903.
9 Iverson, S. J., Springer, A. M., Kitaysky, A. S. 2007 Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids. *Marine Ecology-Progress Series*. **352**, 235-244. (10.3354/meps07073)
10 Barrett, R. T., Asheim, M., Bakken, V. 1997 Ecological relationships between two sympatric congeneric species, Common Murres and Thick-Billed Murres, Uria aalge and U-lomvia, breeding in the Barents Sea. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*. **75**, 618-631.
11 Birkhead, T. R., Nettleship, D. N. 1987*c* Ecological relationships between Common Murres, Uria aalge, and Thick-billed Murres, Uria lomvia, at the Gannet Islands,

Labrador. III. Feeding ecology of the young. *Canadian Journal of Zoology*. **65**, 1638-1649. (doi:10.1139/z87-253)
12 Bryant, R., Jones, I. L., Hipfner, J. M. 1999 Responses to changes in prey availability by Common Murres and Thick-billed Murres at the Gannet Islands, Labrador. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*. **77**, 1278-1287. (10.1139/cjz-77-8-1278)
13 Dorresteijn, I., Kitaysky, A. S., Barger, C. P., Benowitz-Fredericks, Z. M., Byrd, G. V., Shultz, M. T., Young, R. C. Climate variability affects food availability to planktivorous least auklets, *Aethia pusilla*, through physical processes in the southeastern Bering Sea. *Marine Ecology-Progress Series*. **In Press**
14 Anderson, P. J., Piatt, J. F. 1999 Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology-Progress Series*. **189**, 117-123. (10.3354/meps189117)
15 Benowitz-Fredericks, Z. M., Shultz, M. T., Kitaysky, A. S. 2008 Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. *Deep Sea Research Part II: Topical Studies in Oceanography*. **55**, 1868-1876. (doi: 10.1016/j.dsr2.2008.04.007)
16 Inger, R., Bearhop, S. 2008 Applications of stable isotope analyses to avian ecology. *Ibis*. **150**, 447-461.
17 Williams, C. T., Buck, C. L., Sears, J., Kitaysky, A. S. 2007 Effects of nutritional restriction on nitrogen and carbon stable isotopes in growing seabirds. *Oecologia*. **153**, 11-18. (doi:10.1007/s00442-007-0717-z)
18 Kaeriyama, M., Nakamura, M., Edpalina, R., Bower, J. R., Yamaguchi, H., Walker, R. V., Myers, K. W. 2004 Change in feeding ecology and trophic dynamics of Pacific salmon (Oncorhynchus spp.) in the central Gulf of Alaska in relation to climate events. *Fisheries Oceanography*. **13**, 197-207.
19 Schell, D. M., Barnett, B. A., Vinette, K. A. 1998 Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort seas. *Marine Ecology-Progress Series*. **162**, 11-23.

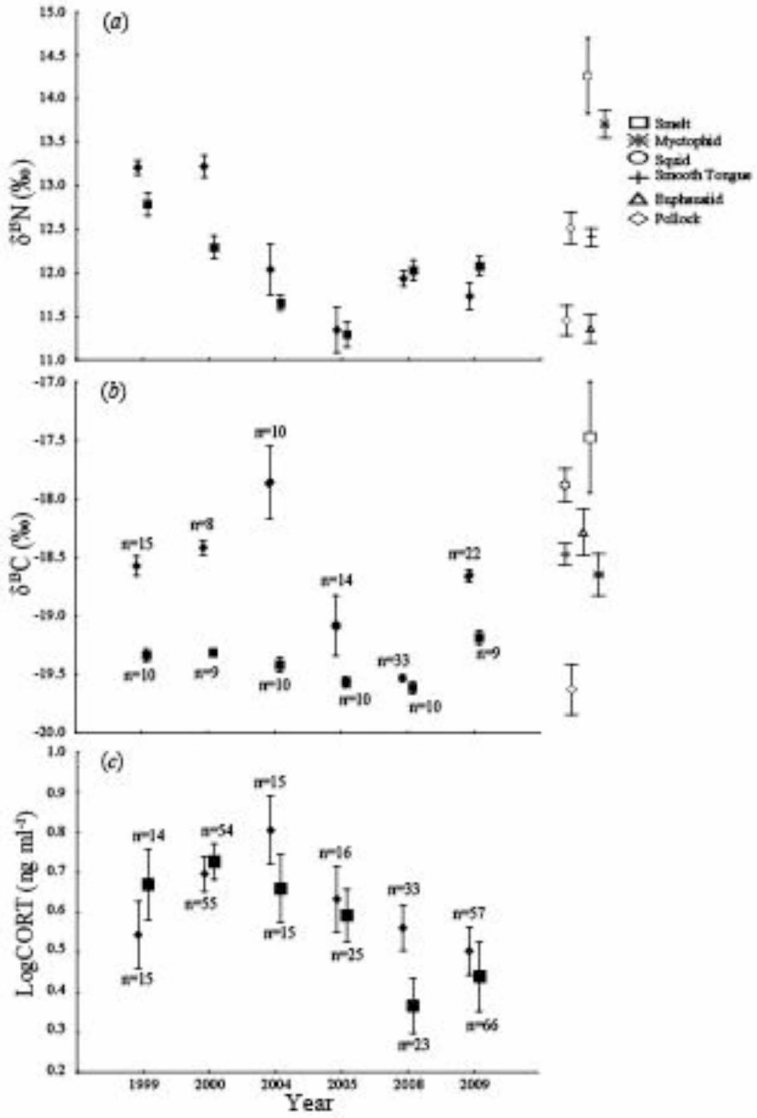

Figure 1.1. Stable isotope and corticosterone of common and thick-billed murres. Interannual changes in SI and CORT (mean ± se) of common (filled circles) and thick-billed murres (filled squares): (*a*) $\delta^{15}N$ values, (*b*) $\delta^{13}C$ values and (*c*) log baseline corticosterone. Sample sizes (n) are shown next to symbols (n were identical for $\delta^{15}N$ and $\delta^{13}C$). SI of the potential prey are reported to illustrate isotopic scope of the food-web (assuming enrichment coefficients of 2.0‰ for $\delta^{15}N$ and 1.0‰ for $\delta^{13}C$).

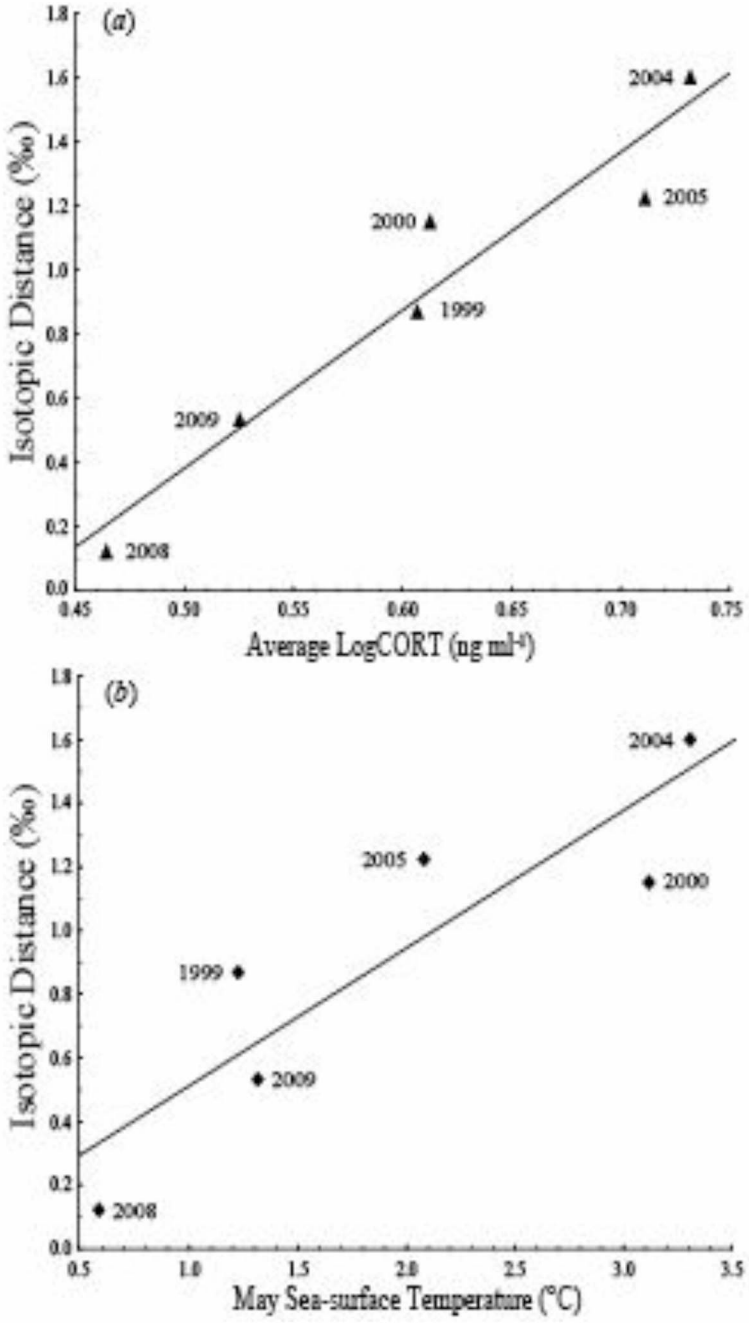

Figure 1.2. Isotopic distance, nutritional stress and May sea-surface temperature. The relationships between interspecific isotopic distance and (*a*) nutritional stress (logCORT, mean ± se; CORT pooled for both species on annual basis; and (*b*) May sea-surface temperature in the SE Bering Sea. Numbers next to symbols indicate year of collection.

Appendix 1.1. Stable isotope values of red-blood cells, corticosterone levels, and isotopic distances. For both Common (COMU) and Thick-billed (TBMU) murres breeding on Bogoslof I. during 1999-2009, and corresponding annual mean May sea surface temperature measurements in the south-eastern Bering Sea.

Year	Species	$\delta^{13}C$ (‰) mean± SE	$\delta^{13}N$ (‰) mean± SE	Corticosterone (ng/ml^{-1}) Log mean± SE	Isotopic Distance (‰)	Mean May SST (°C)
1999	COMU	-18.57±8.08	13.21±0.08	0.54±0.09	0.87	1.22
	TBMU	-19.33±0.05	12.79±0.13	0.67±0.07		
2000	COMU	-18.41±0.06	13.22±0.13	0.70±0.05	1.224	2.07
	TBMU	-19.31±0.02	12.30±0.13	0.73±0.04		
2004	COMU	-17.86±0.31	12.04±0.3	0.80±0.07	1.6	3.29
	TBMU	-19.42±0.06	11.66±0.08	0.66±0.08		
2005	COMU	-19.08±0.26	11.35±0.26	0.63±0.11	1.151	3.1
	TBMU	-19.56±0.05	11.30±0.14	0.59±0.08		
2008	COMU	-19.53±0.02	11.94±0.09	0.56±0.06	0.123	0.59
	TBMU	-19.61±0.05	12.03±0.12	0.37±0.05		
2009	COMU	-18.66±0.05	11.73±0.15	0.59±0.05	0.533	1.31
	TBMU	-19.18±0.06	12.08±0.11	0.46±0.04		

Appendix 1.2. List of prey stable isotope ratios. Prey were collected in the vicinity of Bogoslof Island in late July – early August of 2009, sample size (# of mid-water trawls), and corresponding stable isotope values of whole lean body tissues of prey.

Species	Common Name	Sample Size	$\delta^{13}C$ (‰) mean ±SE	$\delta^{13}N$ (‰) mean ±SE
Gonatopsis borealis	Squid	20	-18.85±0.14	10.51±0.18
Thaleichthys pacificus	Smelt	3	-18.48±0.48	12.21±0.61
Theragra chalcogramma	Walleye Pollock	16	-20.60±0.22	9.44±0.17
Thysanoessa spinifera	Euphausiid	12	-19.25±0.20	9.35±0.17
Leuroglossus schmidti	Smooth Tongue	5	-19.41±0.09	10.40±0.10
Stenobrachius leucopsarus	Myctophid	5	-19.63±0.20	11.70±0.16

CHAPTER 2

RESOURCE PARTITIONING BETWEEN SYMPATRIC SEABIRD SPECIES INCREASES DURING CHICK-REARING[1]

SUMMARY

1. Food resource partitioning by potentially competing species of seabirds may increase during periods of food shortages and increased energy demands. Here we examined whether resource partitioning between common (COMU, *Uria aalge*) and thick-billed (TBMU, *U. lomvia*) murres breeding on the same colony in the Bering Sea increases with a predictable increase in energy demands between the incubation and chick-rearing stages of reproduction. Food shortages are unpredictable and force individuals to seek alternative resources that allow them to restore energy balance (Reactive Response Strategy). Predictable life history events (i.e. raising young) also create increases in energy demands, and parents may anticipate these predicted responses and change their foraging behavior without requiring a triggering stressor (Proactive Response Strategy).
2. Inter-specific food resource partitioning can be manifested by the use of different foraging habitats (segregated spatially and/or temporally), and consumption of different

[1]Barger, C. P., R. C. Young, J. M. Cable, M. Ito, & A. S. Kitaysky. Resource partitioning between sympatric seabird species increases during chick-rearing. Prepared for Functional Ecology.

prey species captured in the same foraging areas. We assessed seasonal dynamics of food availability via corticosterone (CORT) levels, and examined adult diet (via stable isotope analysis of nitrogen and carbon, SI) and chick diets (based on direct nest observations). During chick-rearing, we compared chick-provisioning patterns and examined characteristics of parental foraging habitat via deployment of bird-borne temperature-depth recorders.

3. We found that CORT levels remained low and similar between the species and reproductive stages reflecting relatively stable and favorable foraging conditions for both murre species during reproduction. Comparisons of SI between murres and those of their potential prey indicated a trend that diets were similar between the species during incubation and diverged during chick-rearing. Chick-rearing COMUs and TBMUs used different foraging habitats as reflected in the travel distances to foraging areas and the sea-surface temperature distributions of their foraging dives. TBMUs performed shorter foraging trips and fed their chicks squid, while COMUs foraged farther from the colony and delivered fish to their chicks.

4. These results support a Proactive Response Strategy: food resource partitioning between closely-related murre species breeding in sympatry increased during chick-rearing under favorable foraging conditions. Whether the dietary segregation reflected species-specific differences in adults' foraging efficiency or differences in chicks' dietary requirements remains unknown. Regardless of causal mechanisms involved, food resource partitioning might be adaptive as it would ameliorate inter-specific competition between sympatrically breeding murres during periods of increased energy demands.

Introduction

It is common for various species ranging from plants to mammals to partition resources to different degrees in response to environmental fluctuations and inter-species competition (Pianka 1969; Schoener 1974; Goldberg & Barton 1992). The ecological theory of segregation predicts that multiple species competing for a single resource cannot persist in the same region (Lack 1946; Pianka 1969), and diet partitioning - along spatial, temporal, or prey-type axes - is essential for the co-existence of ecologically similar species. During reproduction, inter-specific food partitioning in animals that share breeding habitat may increase in response to food shortages (Barger & Kitaysky 2012). However, few studies investigating seabirds have addressed if limiting food supply is a required condition for inter-specific dietary segregation. Increases in energy demands associated with raising young impose additional, yet predictable, constraints on parental foraging and may lead to changes in foraging habitat and/or food sources across the breeding season (Ito *et al.* 2010; Wilson 2010). Here we examined patterns of food resource partitioning between sister species of seabirds that often breed side-by-side on the same colonies and are known for substantial variability in their diets (Birkhead & Nettleship 1987; Iverson, Springer & Kitaysky 2007).

Here, we tested whether murres used one of two non-exclusive responses to increases in energy demand. First, food shortages are highly unpredictable and might force individuals to seek alternative sources of food that would allow them to restore and maintain energy balance (hereafter termed the Reactive Response Strategy). When energy availability in the environment declines, birds usually respond by increasing

secretion of the stress hormone corticosterone (CORT; e.g. Kitaysky et al. 2007; 2010), which in turn mediates changes in foraging behavior (Angelier *et al.* 2007; Angelier *et al.* 2009; Barger & Kitaysky 2012). Our previous studies demonstrated that during the incubation stage of reproduction, lowered food availability results in increased stress levels, and breeding adult murres partition their food resources, resulting in larger stable isotopic differences during food limited periods (Barger & Kitaysky 2012). This pattern of lowered food availability, increased stress, and changed behavior supports our Reactive Response Strategy, however this pattern has not been examined during chick provisioning. The Reactive Response Strategy predicts that an increase in nutritional stress is required to drive a change in diet composition: murre are "reacting" to an internal stressor caused by external circumstances. Second, when life history stages create expected increases in energy demands, birds can change food resources facultatively without a stress response. The shift from incubation to chick provisioning is a common example of an increase in energy demands in breeding birds (Monaghan *et al.* 1989; Croll 1990; Montevecchi, Birt-Friesen & Cairns 1992; Bevan *et al.* 1995). We term this anticipatory behavioral response, which does not depend on an internal stress level cue, the Proactive Response. A Proactive Response Strategy requires parents to adjust behavior to optimize self-foraging (Williams, Iverson & Buck 2008) and specific requirements of their young (Markman, Pinshow & Wright 1999) without a nutritionally-driven increase in stress hormones. Both mechanisms may lead to a change in food resources to reconcile a disparity between the energy available to murres in the

environment and energy required for self-maintenance and reproductive activities. These adjustments may also result in partitioning of the trophic niche.

In seabirds, partitioning of food resources has been found to occur spatially and/or temporally, with or without differences in diet composition (Wilson 2010). The extent of resource partitioning, such as flight distances and vertical location of prey, may be critical for energetically constrained seabirds with high travel costs (Gaston 1985). Many seabirds, and especially pursuit-divers, have high wing loading (Pennycuick 1987), which drastically increases the energy expenditure as foraging distances increase. The focal species in our study, the common (*Uria algae*) and thick-billed murre (*U. lomvia*), deliver only a single prey item per foraging trip; therefore optimization of provisioning efficiency is essential (Birkhead & Nettleship 1987). Chick-rearing is a time of high energetic demands on parents, and these increased demands may cause murres to alter their foraging strategy to accommodate chick requirements (Monaghan *et al.* 1989; Croll 1990; Montevecchi, Birt-Friesen & Cairns 1992; Deagle, Gales & Hindell 2008; Ito *et al.* 2010). Evidence for changes in foraging behavior during chick-rearing has been found in murres (Ito et al. 2010) and other species (e.g.(Weimerskirch & Cherel 1998; Williams, Iverson & Buck 2008)); however, it is not well understood whether these changes are related to inter-specific resource partitioning. Advances in portable recording devices, like temperature-depth recorders (TDRs) make it possible to disentangle spatial and temporal foraging areas. Here, we study resource partitioning by examining variability in use of different water masses for foraging (detected by water temperature), depth of prey capture, and trip duration (established via return flight times). The literature support

these variables as strong indicators of partitioning and habitat use in seabirds (Mitani *et al.* 2003; Spear & Ainley 2007; Masello *et al.* 2010).

We used plasma concentrations of the adrenal hormone corticosterone (CORT) as an indirect measure of prey availability. Previous studies have shown CORT to be an effective proxy for relative changes in prey availability in seabirds; CORT shows increases in relative concentrations during periods of food shortages (Wingfield, Vleck & Moore 1992; Kitaysky, Wingfield & Piatt 1999; Kitaysky, Piatt & Wingfield 2007; Doody *et al.* 2008; Kitaysky *et al.* 2010; Dorresteijn *et al.* 2012; Satterthwaite, Kitaysky & Mangel 2012). To compare diets of adults, we examined stable carbon and nitrogen isotope values ($\delta^{13}C$ and $\delta^{15}N$) of blood (Thompson *et al.* 1999; Cherel *et al.* 2008; Inger & Bearhop 2008). This method can be responsive to changes in diet or habitat selection depending on the variability in prey stable isotope (SI) values (see potential prey SI values in Barger and Kitaysky 2012) and has been used in past studies of seabird foraging ecology (Thompson *et al.* 1999; Navarro *et al.* 2009).

The goal of this paper is to determine if resource partitioning between common and thick-billed murres change between the incubation and chick-rearing stages of reproduction. To compare inter-specific differences in the diet composition of adult birds, we estimated the contribution of potential prey species, captured in the vicinity of the breeding colony, based on analysis of stable isotope ratios of blood and potential prey using a Bayesian mixing model (Cable, Ogle & Williams 2011). To compare chick diet compositions, we directly observed prey delivered to chicks. To examine inter-specific differences in spatial and temporal variability of the foraging habitat use, we deployed

TDRs on adult murres during the chick rearing. Previous studies have shown this to be an effective tool at delineating slight differences in water masses and foraging ecology between seabird species (Ito *et al.* 2010; Wilson 2010). By combining these informative tools, we aimed to delineate the resource partitioning between murre species, both spatially and temporally, in response to an increase in energy demands during chick-rearing.

Methods

Study Site, Bird Capture, and Data Logger Usage

This study was conducted on Bogoslof Island (53°55′38″N 168°02′04″W) in 2009. Bogoslof Island is located ca. 40 km north of the Aleutian chain in the Bering Sea. Incubating (COMU n=11, TBMU n=10) and chick-rearing (COMU n=31, TBMU n=36) birds were captured (with telescopic noose poles) at their nesting sites in mixed colonies of common and thick-billed murres (for details of bird capture methods see (Benowitz-Fredericks, Shultz & Kitaysky 2008)). In 2009, murres arrived in the vicinity of Bogoslof in early April (Orben *et al.* 2012), laid eggs in late June (the incubation duration usually ranges between 26 and 39 days), hatched chicks in early August (Ainley *et al.* 2002; Klostermann, Scopel & Drummond 2011; Orben *et al.* 2012), and the majority of birds fledged their chicks by early September (CPB *pers comm.*). During sampling, all birds were banded with US Fish and Wildlife metal bands, and no individuals were sampled twice. Blood samples were collected from the brachial vein within three minutes of capture, with the capture time defined as the second the bird had contact with the monofilament noose. Samples collected within this time frame reflect

baseline CORT levels (Romero & Reed 2005; Kitaysky, Piatt & Wingfield 2007; Benowitz-Fredericks, Shultz & Kitaysky 2008). During chick-rearing, we placed temperature-depth recording data loggers (diameter: 8mm, length: 30mm, weight in air: 2.7g; Cefas G5, Cefas Technology) on common (n = 11) and thick-billed murres (n=28).

Blood sampling and Hormone Analysis

Blood samples of common and thick-billed murres were collected using a heparinized syringe or heparinized needles with microhematocrit tubes, transferred to 0.5 ml microcentrifuge tubes, and stored on ice until centrifugation; usually no more than 8 hours post collection. Whole blood samples were centrifuged for 5 min to separate plasma and red blood cells. The plasma was removed and stored frozen until CORT assays. Plasma concentrations of CORT were determined via radioimmunoassay as previously described (Romero & Reed 2005; Kitaysky, Piatt & Wingfield 2007; Benowitz-Fredericks, Shultz & Kitaysky 2008). Inter and intra-assay variability coefficients were less than 6% and 2%, respectively.

Stable Isotope Analysis

Red blood cells from common and thick-billed murres were used for stable carbon and nitrogen isotope analysis. SI ratios in lean whole body tissue of prey were determined as previously described (Williams *et al.* 2007). A small portion of freeze-dried samples (0.100 – 0.400 mg) were placed in a tin capsule, sealed and deposited in an EA autosampler. The stable isotope data was obtained using continuous-flow isotope ratio mass

spectrometry (CF-IRMS). The instrumentation used was a Delta+XP isotope ratio mass spectrometer (Thermo Electron) interfaced with a Costech ESC 4010 elemental analyzer. Stable isotope ratios were reported in "δ" notation as parts per thousand (‰) deviation from the international standards $\delta^{13}C_{PDB}$ and $\delta^{15}N_{air}$, as follows: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000‰$, where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Replicate measures of internal laboratory standard (Peptone) indicated measurement errors to be ± 0.16‰ N and ± 0.13‰ for C. Samples were analyzed at the University of Alaska Fairbanks Stable Isotope Facility.

Chick Diet and Parental Time Budgets

Murres typically forage for themselves and then bring a single prey item back to the colony for their chick. Prey delivered to chicks are held in the beak and usually a large portion is visible for identification (Birkhead & Nettleship 1987). We conducted two 18-hour observation periods for common murres and three similar observation periods for thick-billed murres. In each study plot, 12-15 pairs were marked in a non-toxic cattle dye such that we could observe specifically marked individuals and distinguish between the parents at a single nest. During nest watches, each pair was observed continuously and prey items were photographed and identified to the lowest taxonomical level possible.

Data logger deployment and analysis

TDR data loggers (G5 Cefas Technology) were set to record temperature and pressure (depth) at 2s intervals with a temperature and depth resolution of 0.1°C and 0.1m,

respectively. In order to reduce the instrument impacts on flight and diving behavior, loggers were attached to the keel feathers with Tesa® tape (Tremblay *et al.* 2003; Takahashi *et al.* 2008a; Ito *et al.* 2010). Birds with data loggers had a blood sample drawn at initial capture, were banded and measured, and were released within 10min. Upon re-capture of the bird, diving and temperature data were downloaded from loggers to a computer using G5 Host, Cefas Technology.

The analyses of diving profiles were conducted using Igor Pro software (Wave Metrics). Dive depth, temperature (sea-surface temperature), and trip duration were determined for each dive track. Foraging trip duration was determined from the timing of the temperature drop associated with colony departure to a return to temperature indicative of presence at the colony (equal or higher than 15°C). To estimate the duration of flight from the foraging ground, we extracted flight times from the end of last dive until an individual's return to the colony. Sea surface temperatures (SST) were calculated by using a custom-written script (developed by Ito *et al* 2010) in Igor Pro that calculated the SST after each dive.

Statistical analyses

To address changes in resource partitioning between species as the breeding season progressed from incubation through chick-rearing, we used three separate general linear models (GLMs) to determine differences in baseline CORT, $\delta^{13}C$, and $\delta^{15}N$ between species and stage (incubation or chick-rearing). Baseline CORT data were log transformed to meet the assumptions for parametric statistical comparisons. To assess

differences in chick diets between the species we used Chi-squared tests. We compared attendance (time spent at the colony), foraging trip durations, and chick-feeding rates obtained from observations among species using a normal linear mixed model, with species as a fixed factor, individual as a random factor and Julian date as a covariate. For comparisons of diving data, we used separate normal linear mixed models to test if birds were using different water masses (SST per dive), maximum dive depth, trip durations (a time period between departure and subsequent return of an individual to the colony), and flight times from the end of last foraging bout to arriving at the colony. For each model, species was included as a fixed factor and individual identity was included as a random factor. To test how the usage of different water masses (as reflected in the SST of each diving bout) and maximum diving depths changed over the course of the day, time of day was included in the models as a continuous variable. To test whether murres differed in frequencies of their dives over the course of the day we used Kolmogorov-Smirnov two-sample test on frequencies of dives performed by individuals over time of the day. We used a *t*-test on arcsin-transformed proportions of dives performed by each individual during the night-time period (see below) to compare diving frequencies between species during the night- and day-time periods. We determined the night and day periods based on direct observations of the colony attendance behavior of chick-rearing murres. As we have never observed murres arriving at the colony after mid-night and prior to 7am in the morning, we deemed it as the "night time" and the remaining part of the day as the "day time" period. Our definition of the night and day periods also corresponds to the timing of sunset (2439-0121) and sunrise (0915-0953) in the study region from 25 July to

August 16 (www.NOAA.gov). All statistical analyses were preformed using Statistica (v.10.0) and R (v.2.11.1, R Foundation for Statistical Computing (Hornik 2012)). Data are presented as means ± SE unless otherwise specified.

Dietary analysis based on stable isotope ratios

Following Cable *et al.* (2011), a Bayesian approach was used to infer murre diet compositions based on the stable isotope signatures of bird red blood cells (RBC) and those of their potential prey. Using these methods, we estimated diet during both incubation and chick-rearing. We assumed that RBC isotope measures during incubation were in equilibrium with the diet as available evidence suggests that murres are foraging in the vicinity of breeding colonies at least 2.5 months prior to egg-laying (Ainley *et al.* 2002; Orben *et al.* 2012). Assuming that a dietary shift occurred in all individuals at the beginning of the chick-rearing stage, isotope measures taken early in chick-rearing were not in equilibrium with the diet. To make a conservative estimate of adult diets during chick-rearing, we have chosen only individuals (11 COMUs, and 10 TBMUs) that had completed at least 50% turnover at the date of sampling (36 days since the start of the chick-rearing stage). To determine 50% turnover, we used a fractional turnover rate of (0.018), based on the previously reported allometric relationship between body mass and stable isotope turnover rates in blood (Bauchinger & McWilliams 2009; Martínez del Rio & Carleton 2012). The Bayesian mixing model combines the likelihoods for the observed $\delta^{13}C$ and $\delta^{15}N$ data from the sources (N = 7 potential prey species) caught in the vicinity of the colony concurrent with sampling of chick-rearing birds. We used SI ratios

of the main potential prey species (see table in appendix 1.1 and 1.2 as reported in Barger & Kitaysky 2012) collected in the proximity of the colony in 2009 (Whitman 2010).

We assigned the data to a bivariate normal distribution (*MNormal*, expression (1)) with a mean vector ($\mu = [\delta^{13}C_{src}, \delta^{15}N_{src}]$) and a precision matrix (Ω_{src}), which is the inverse of the covariance matrix. The multivariate normal accounts for correlations between the residual errors for the $\delta^{13}C$ and $\delta^{15}N$ data. For observation j, (j = 1, 2, … Nsrc) for each source *src*:

$$\begin{bmatrix} \delta^{13}C_{src} \\ \delta^{15}N_{src} \end{bmatrix}_{\{j\}} \sim MNormal\left(\begin{bmatrix} \mu\delta^{13}C_{src} \\ \mu\delta^{15}N_{src} \end{bmatrix}, \Omega_{src} \right) \quad (1)$$

The means (μ's) for the seven potential prey species are assigned noninformative independent priors, and the precision matrices for the sources are assigned the same noninformative Wishart priors.

$$\begin{aligned} \mu\delta^{13}C_{src}, \mu\delta^{15}N_{src} &\sim Normal(0, 0.00001) \\ \Omega_{src} &\sim Wishart(R, 2) \end{aligned} \quad (2)$$

Note that R in expression (2) is the 2x2 identity matrix, and the "2" represents the minimum "degrees of freedom," this parameterization gives the most non-informative prior for Ω_{src}. Enrichment factors for $\delta^{13}C$ and $\delta^{15}N$ were added to the predicted mean isotope value for each source. The mean and precisions for the priors of the enrichment factors were determined using the equations provided by Caut *et al.* (2009); a mean of 2.25 and standard deviation (σ) of 0.2 (precision (τ) of 25, $\tau = \sigma^{-2}$) was reported for N. The enrichment factors we estimated based on Caut (2009) were extremely similar to enrichment factors reported in Williams (2007), where they determined fractionation

factors at 2.28‰ for $\delta^{15}N$ and -0.50‰ for $\delta^{13}C$ for tufted puffins (*Fratercula cirrhata*) that belong to the same family Alcidae as our focal species. An equation was provided to calculate the mean for $\delta^{13}C$ ($\delta^{13}C$ = -0.1999* (mean $\delta^{13}C$) - 3.989), where the mean $\delta^{13}C$ is the average of the $\delta^{13}C$ values of the birds. We assumed that the $\delta^{13}C$ enrichment factor has the same standard deviation (precision) as $\delta^{15}N$. We used a precision of 15 (σ = 0.26), which allows the data to inform the enrichment factors to a greater degree than a precision of 25. Thus, the priors for the enrichment factors were: $\delta^{15}N_{enr} \sim$ *Normal*(2.25, 15) and $\delta^{13}C_{enr} \sim$ *Normal*(-0.379, 15). The estimated enrichment factors were close to the mean (as expected with informative priors) and similar to those reported in other studies (Becker *et al.* 2007; Williams *et al.* 2007; Cherel *et al.* 2008).

The likelihood for the bird isotope signatures also follow a bivariate normal distribution with a mean vector ($\mu_{bird} = [\delta^{13}C_{bird}, \delta^{15}N_{bird}]$) and a precision matrix (Ω_{bird}). For observation j (j = 1, 2, …. N_{birds}), incubation stage year y and species s:

$$\begin{bmatrix} \delta^{13}C_{bird} \\ \delta^{15}N_{bird} \end{bmatrix}_{\{i\}} \sim MNormal\left(\begin{bmatrix} \mu\delta^{13}C_{bird} \\ \mu\delta^{15}N_{bird} \end{bmatrix}_{\{y,s\}}, \Omega_{bird} \right) \quad (3)$$

The mean stable isotope values for the birds are given by a mixing model, which defines the mean values as the sum of the fractional contribution (p) of each prey source multiplied by each source's expected isotope signature (i.e., the μ's in eqn 1):

$$\begin{bmatrix} \mu\delta^{13}C_{bird} \\ \mu\delta^{15}N_{bird} \end{bmatrix}_{\{y,s\}} = \sum_{src} p_{src_{\{y,s\}}} \cdot \begin{pmatrix} \mu\delta^{13}C_{src} \\ \mu\delta^{15}N_{src} \end{pmatrix} \quad (4)$$

To satisfy the mass-balance constraints, $0 \le p_{src} \le 1$ and $p_1 + p_2 + p_3 + p_4 + p_5 + p_6 + p_7 = 1$, we modeled the vector of seven p's for a given year and species as coming from a

Dirichlet distribution with parameter vector $\alpha = (\alpha_1 + \alpha_2 + \alpha_3 + \alpha_4 + \alpha_5 + \alpha_6 + \alpha_7)$ (7 sources) (Semmens *et al.* 2009; Parnell *et al.* 2010). The Dirichlet distribution gives the mean (or expected value, *E*) of each source-specific *p* as $E(p_{src}) = \alpha_{src}/(\alpha_1 + \alpha_2 + \alpha_3 + \alpha_4 + \alpha_5 + \alpha_6 + \alpha_7)$.

We implemented the HB model in OpenBUGS, a free software package for Bayesian data analyses (Lunn *et al.* 2000). We ran three parallel MCMC (Markov chain Monte Carlo) chains for 20,000 iterations. We discarded the first 5,000 samples as a burn-in period (prior to convergence of the chains), resulting in a total of 15,000 samples for calculating the posterior statistics.

Results

Corticosterone (CORT) Analysis

Baseline CORT levels were relatively low (common murres: 4.86 ± 0.58 ng ml^{-1}; thick-billed murres: 3.63 ± 0.33 ng ml^{-1}) and similar between the species ($F_{1,115} = 2.35$, $p = 0.128$) and stages ($F_{1,114} < 0.001$, $p = 0.978$). The species × stage interaction term was not significant ($F_{1,114} = 0.50$, $p = 0.479$), and the Julian date effect was also not significant ($F_{1,114} = 1.82$, $p = 0.180$).

Stable Isotope Analysis and Bayesian Model output

Isotope ratios changed over time (stats, Fig 1). Measured stable isotope signatures were different between incubation and chick-rearing ($\delta^{13}C$: $F_{1,74} = 12.7$, $p < 0.001$; $\delta^{15}N$: $F_{1,74} = 12.63$, $p < 0.001$; Fig. 2.1) and between species for carbon values ($\delta^{13}C$: $F_{1,74} = 65.5$, $p < 0.001$) but not for nitrogen values ($\delta^{15}N$: $F_{1,74} = .93$, $p = 0.337$). Differences in stable

isotope signatures between stages differed between species ($\delta^{13}C$: $F_{1,74} = 4.8$, $p = 0.031$; $\delta^{15}N$: $F_{1,74} = 22.88$, $p < 0.001$).

Using the Bayesian mixing analysis, we modeled the fractional contribution (mean and 95% credible interval) of 7 prey items known to contribute to diets of murres in the North Pacific (Fig 2.2). Given the limited number of data points for some of the prey items (e.g., 3 data points for the pacific smelt, *Osmeridae*, see Table in Appendix in Barger and Kitaysky 2012), the credible intervals on the posterior estimates for the fractional contribution of the different prey items were somewhat large. However, the results suggest that during the incubation stage for both species of murres, Arctic Squid, Arrowtooth Flounder, and euphasiids were more important prey items than Northern Lampfish, Northern Smooth Tongue, and Walleye Pollock (Fig. 2.2). During the chick-rearing stage, Arrowtooth Flounder, Arctic Squid and Pacific Smelt were probably the most important prey of adult common murres, while Arctic squid, Arrowtooth Flounder, Walleye Pollock and euphausiids were probably the most important prey of adult thick-billed murres (Fig. 2.2).

Chick Diets

A total of 184 prey items were observed between the two species and 98% were identified to the genus/family. The remaining 2% were classified as unidentified because the observer's view of the prey delivered was obscured or the rate of delivery was too rapid. The proportion of fish and squid in chick diets differed between species ($\chi^2 = 13.56$, $df = 2$, $p < 0.001$). Common murre chicks were primarily (91%) fed schooling

fish *Osmeridae*, whereas thick-billed murre chicks received primarily squid (89%) and only a small percentage of their diet was composed of fish (Fig. 2.3).

Chick provisioning rates were also different between the species: thick-billed murre chicks were fed 4–5 items per 18hr observational period (0.244 ± 0.008 feeds per hour, n = 113) compared to common murre chicks that were fed less frequently (2–3 items per 18 h observational period) at the rate of 0.156 ± 0.012 (feeds/hour, n = 71; $F_{1,55}$ = 23.27, $p < 0.001$).

Foraging habitat

Trip duration A significant inter-specific difference in the foraging trip duration was detected (Fig. 4). Direct observations of nests showed that thick-billed murres performed shorter forging trips compared to those of common murres (thick-billed murre 174 ± 6.18 min, n = 82; common murre 353 ± 22.13 min, n = 43; $F_{1,36}$ = 5.67, p = 0.023). TDR data also showed that thick-billed murres performed shorter forging trips compared to those of common murres ($F_{1,35}$ = 17.34, $p < 0.001$, Fig 2.4).

Foraging distances Based on the flight time from last foraging bout prior to an individual's arrival at the colony (assessed via TDR), thick-billed murres performed shorter flights than common murres (average time COMU: 50.1 ± 5.4 min n=31, and TBMU 15.5 ± 1.6 min n=122; $F_{1,36}$ = 5.67, p = 0.023). Assuming that individuals traveled directly from the location of their last foraging place back to the colony at a speed of

65kmh^{-1} (Benvenuti *et al.* 1998; Takahashi *et al.* 2008b), their estimated average travel distances were ~54 km from the colony for common and ~17 km for thick-billed murres.

Sea surface water temperature and diving profiles Overall SSTs of foraging dives were not significantly different between species ($F_{1,30} = 1.9$, $p = 0.18$); and time of day had no directional effect on SSTs ($F_{1,15515} < 0.0$, $p = 0.995$). However, the usage of water masses was different between the species with common murres foraging in warmer waters at night and colder waters during daytime compared to thick-billed murres (time of day X species; $F_{1, 15515} = 56.19$, $p < 0.001$; Fig. 2.5, low panel).

Overall maximum diving depths were not significantly different between the species ($F_{1,37} = 5.31$, $p = 0.337$). Time of day had a significant effect on maximum diving depths ($F_{1,23032} = 1115.19$, $p < 0.001$). The temporal dynamics of diving depths were also different between the species (time of day X species; $F_{1,23032} = 115.57$, $p = <0.001$) with common murres diving shallower during daytime and deeper at night compared to thick-billed murres (Fig. 2.5, middle panel).

Overall temporal changes in frequencies of all foraging dives were different between the species (Kolmogorov-Smirnov $D = 43.77$, $p < 0.001$; Fig. 5 upper panel). Thick-billed murres performed a higher proportion of dives at night ($t_{31} = 3.62$, $p < 0.001$) and lower proportion of dives during day time compared to common murres (Fig 2.5, upper panel).

Discussion

In this study, we examined how two closely related species partitioned available food resources during incubation and chick-rearing. We found that the diets of common and thick-billed murres were similar during incubation and diverged during chick-rearing. Chick-rearing murres used different foraging habitats and pursued different foraging strategies: thick-billed murres foraged in close proximity to the colony and primarily delivered squid to their young, while common murres foraged farther from the colony and fed their chicks with schooling fish. The primary prey species consumed by adult common and thick-billed murres also differed during chick rearing. This apparent partitioning of foraging resources was not influenced by food limitations experienced by breeding birds, as nutritional stress levels of parents were low in both species and did not change throughout the breeding season.

Adult diets Murres breeding on Bogoslof I. in 2009 appeared to utilize a variety of foraging habitats both spatially and temporally. During incubation, adults of both species had similar isotopic signatures suggesting their reliance on similar prey resources and habitats. Bayesian modeling predicted that both species fed on a large spectrum of available prey including squid, arrowtooth flounder, and euphausiids. However, as parents transitioned from incubation to chick-rearing, a concurrent shift in adult diets occurred in both species. A comparison of stable isotope signatures of chick-rearing murres and their potential prey suggested that common murres were consuming mostly arrowtooth flounder, arctic squid, and/or pacific smelt, while thick-billed murres were

consuming euphausiids, arctic squid, and/or walleye pollock (Fig. 2.2). Across chick rearing the trend of increasing $\delta^{15}N$ signatures of chick-rearing common murres (Fig. 2.1a) is also suggestive that parents switched from lower trophic level prey (probably euphausiids) during incubation to higher trophic level prey during chick-rearing (Fig. 2.1a). Even though the SI ratios were not in complete equilibrium with the diet at time of sampling, there is still a clear shift in SI ratios during this time period. Several studies suggest that enrichment of $\delta^{15}N$ values occurs when food shortages result in starvation and metabolism of body proteins (Oelbermann & Scheu 2002). However, this was not supported by our measures of physiological stress incurred by breeding birds. CORT levels remained relatively low (for example, CORT levels of common and thick-billed murres measured at the same colony in 2004 were twice as high as in 2009, see Barger & Kitaysky 2012 for inter-annual comparisons) and stable throughout the reproductive season in both species, indicating little nutritional stress, and $\delta^{15}N$ values increased in common but not thick-billed murres. Therefore, we believe that $\delta^{15}N$ signatures reflected changes in diets rather than nutritional stress of common murres.

Based on observed changes in $\delta^{15}N$ and $\delta^{13}C$ signatures of blood in adults, we conclude that as common and thick-billed murres transitioned from incubation to the chick-rearing stage of reproduction they started using different prey and foraging habitats for self-feeding, and both species maintained low physiological stress. Although niche theory predicts that similar species would always segregate resources (Lack 1946; Pianka 1969), murres have been shown to utilize similar prey species in some areas/years and demonstrate strong foraging differences in others (Birkhead & Nettleship 1987; Barrett,

Bakken & Krasnov 1997; Barger & Kitaysky 2012). Previous studies suggested that common murres might be specializing in foraging on fish species whereas thick-billed murres are more generalist foragers (Birkhead & Nettleship 1987). Results of this study supported this difference in specialization but also showed that foraging preferences of both murre species may change between incubation and chick-rearing stages of reproduction.

Spatial and temporal partitioning of foraging habitat Chick-rearing common and thick-billed murres relied on different food resources for self-feeding and chick-provisioning, however, they could have continued to use the same foraging habitat (Wilson 2010). Our results suggest that this was not the case. Specifically, we found evidence for spatial segregation: (1) foraging in different water masses as reflected in SST; (2) differences in foraging trip durations and travel time between foraging grounds and the breeding colony. We also found evidence for temporal segregation: (1) species foraged in waters with different SST depending on time of the day; and (2) thick-billed murres' diving frequency peaked during the night hours, while common murres' diving frequency peaked during the day time hours. Altogether, results of this study suggest that in response to an increase in energy demands, two species increased partitioning of food resources by consuming different prey captured in different foraging habitats.

Species-specific foraging strategies Organisms with large niche overlap should strictly partition their foraging habitat when experiencing an energy deficit, induced by either

food shortages (resulting in less energy available from the environment, i.e. see Barger & Kitaysky 2012) or an increase in organismal energy demands (this study). During the breeding season, central place foragers, such as murres, are expected to forage optimally by balancing the length of their foraging trips with the energy content of prey delivered to young (Kacelnik 1984). In this study, we found that the focal species used two different foraging strategies to achieve this balance. Common murres were taking longer foraging trips and foraging farther away from the colony, while thick-billed murres were taking shorter trips and foraged closer to the colony. According to the predictions of optimal foraging theory, we expected that chick-rearing individuals performing longer foraging trips would deliver more energy-rich prey items to their young compared to individuals that perform shorter foraging trips. However, previous studies (Whitman 2010) have found that, in the study region, the *Osmeridae* species of schooling fish (a prevalent food of common murre chicks in our study) and squid (main food of thick-billed murre chicks) are relatively similar in their energy densities per prey item (also see (Cherel & Ridoux 1992; Van Pelt *et al.* 1997; Hedeholm, Grønkjær & Rysgaard 2011). This observation implies that despite apparently larger foraging effort, common murres were not delivering more energy per trip than thick-billed murres. Thick-billed murre chicks might require higher feeding rates than COMU chicks due to an additional energy expenditure associated with a squid diet. Marine fish and invertebrates differ in their salt content: squid contain more salt (iso-osmotic to their environment) than fish (hypo-osmotic) (Hodum & Hobson 2000). Because murres feed their young whole, undigested prey, thick-billed murre chicks would have to excrete excess salt they receive with squid,

which is an energy-demanding physiological process (Nystrom & Pehrsson 1988; Dosch 1997; Hodum & Hobson 2000; Hedeholm, Grønkjær & Rysgaard 2011). Thus, although common murre chicks were fed less frequently than thick-billed murre chicks, perhaps their energetically more profitable prey (i.e. that does not come at a cost of salt excretion) could compensate for the longer foraging trips and lower feeding rates of common murres. Finally, the species-specific foraging strategies that we observed during chick rearing might be due to differences in foraging specialties of each species. Past studies suggested that common murres are potentially more adept at foraging for fish, whereas thick-billed murres are suited for capturing a variety of invertebrate and fish species (Birkhead & Nettleship 1987). Such foraging specializations of adults could contribute to prey choice and dietary segregation of murres during a period of increased energy demands.

Conclusions In this study we observed a shift in diet composition during increased demands of chick-rearing, supporting a Proactive Response Strategy. During this reproductive season, food limitations did not appear to be a limiting factor to reproductive success, which allowed us to test this hypothesis. Our results clearly showed that partitioning occurred spatially, temporary, and through selection of different prey. It is plausible that murres have adapted this foraging strategy to avoid inter-specific competition when large energy demands of chick provisioning are anticipated. The species' chosen strategies may reflect either inter-specific difference in foraging efficiencies of parents and/or energy demands of chicks depending on prey type (large

invertebrates versus schooling fish). Regardless of the proximate mechanism, during food shortages (Barger & Kitaysky 2012) or increased energy demands (this study), a mis-match between energy available in the environment and animal's energy demands are likely to lead to an increased partitioning of resources by species of seabirds breeding on the same colonies and using similar foraging niches.

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Literature Cited

Ainley, D.G., Nettleship, D.N., R., C.H. & Storey, A.E. (2002) Common Murre (*Uria aalge*). *The Birds of North America Online (A. Poole, Ed.).* Cornell Lab of Ornithology, Ithaca.

Angelier, F., Clément-Chastel, C., Welcker, J., Gabrielsen, G.W. & Chastel, O. (2009) How does corticosterone affect parental behaviour and reproductive success? A study of prolactin in black-legged kittiwakes. *Functional Ecology,* **23,** 784-793.

Angelier, F., Shaffer, S.A., Weimerskirch, H., Trouve, C. & Chastel, O. (2007) Corticosterone and foraging behavior in a pelagic seabird. *Physiological and Biochemical Zoology,* **80,** 283-292.

Barger, C.P. & Kitaysky, A.S. (2012) Isotopic segregation between sympatric seabird species increases with nutritional stress. *Biology Letters,* **8,** 442-445.

Barrett, R.T., Bakken, V. & Krasnov, J.V. (1997) The diets of common and Brünnich's guillemots Uria aalge and U. lomvia in the Barents Sea region. *Polar Research,* **16,** 73-84.

Bauchinger, U. & McWilliams, S.R. (2009) Carbon Turnover in Tissues of a Passerine Bird: Allometry, Isotopic Clocks, and Phenotypic Flexibility in Organ Size. *Physiological and Biochemical Zoology,* **83,** 1032.

Becker, B.H., Newman, S.H., Inglis, S. & Beissinger, S.R. (2007) Diet-feather stable isotope (delta N-15 and delta C-13) fractionation in Common Murres and other seabirds. *Condor,* **109,** 451-456.

Benowitz-Fredericks, Z.M., Shultz, M.T. & Kitaysky, A.S. (2008) Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. *Deep Sea Research Part II: Topical Studies in Oceanography,* **55,** 1868-1876.

Benvenuti, S., Bonadonna, F., Dall'Antonia, L. & Gudmundsson, G.A. (1998) Foraging flights of breeding thick-billed Murres (Uria lomvia) as revealed by bird-borne direction recorders. *Auk,* **115,** 57-66.

Bevan, R.M., Butler, P.J., Woakes, A.J. & Prince, P.A. (1995) The energy expenditure of free-ranging black-browed albatrosses. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **350,** 119-131.

Birkhead, T.R. & Nettleship, D.N. (1987) Ecological relationships between Common Murres, Uria aalge, and Thick-billed Murres, Uria lomvia, at the Gannet Islands, Labrador. III. Feeding ecology of the young. *Canadian Journal of Zoology,* **65,** 1638-1649.

Cable, J., Ogle, K. & Williams, D. (2011) Contribution of glacier meltwater to streamflow in the Wind River Range, Wyoming, inferred via a Bayesian mixing model applied to isotopic measurements. *Hydrological Processes,* **25,** 2228-2236.

Cherel, Y., Le Corre, M., Jaquemet, S., Menard, F., Richard, P. & Weimerskirch, H. (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. *Marine Ecology-Progress Series,* **366,** 281-291.

Cherel, Y. & Ridoux, V. (1992) Prey species and nutritive-value of food fed during summer to king pernguin aptenodytes-patagonica chicks at possesssion island, crozet archipelago. *Ibis,* **134,** 118-127.

Croll, D.A. (1990) Diving and energetics of the thick-billed murre, *Uria lomvia*. Doctor of Philosophy, University of California, San Diego.

Deagle, B.E., Gales, N.J. & Hindell, M.A. (2008) Variability in foraging behaviour of chick-rearing macaroni penguins Eudyptes chrysolophus and its relation to diet. *Marine Ecology-Progress Series,* **359,** 295-309.

Doody, L.M., Wilhelm, S.I., McKay, D.W., Walsh, C.J. & Storey, A.E. (2008) The effects of variable foraging conditions on common murre (Uria aalge) corticosterone concentrations and parental provisioning. *Hormones and Behavior,* **53,** 140-148.

Dorresteijn, I., Kitaysky, A.S., Barger, C., Benowitz-Fredericks, Z.M., Byrd, G.V., Shultz, M. & Young, R. (2012) Climate affects food availability to planktivorous least auklets Aethia pusilla through physical processes in the southeastern Bering Sea. *Marine Ecology-Progress Series,* **454,** 207-220.

Dosch, J.J. (1997) Salt tolerance of nestling laughing gulls: An experimental field investigation. *Colonial Waterbirds,* **20,** 449-457.

Gaston, A.J. (1985) Energy Invested in Reproduction by Thick-Billed Murres (Uria lomvia). *The Auk,* **102,** 447-458.

Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific competition in natural communities - A review of field experiments with plants. *American Naturalist,* **139,** 771-801.

Hedeholm, R., Grønkjær, P. & Rysgaard, S. (2011) Energy content and fecundity of capelin (<i>Mallotus villosus</i>) along a 1,500-km latitudinal gradient. *Marine Biology,* **158,** 1319-1330.

Hodum, P.J. & Hobson, K.A. (2000) Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope (delta N-15 and delta C-13) analyses. *Marine Ecology-Progress Series,* **198,** 273-281.

Hornik, K. (2012) The R FAQ.

Inger, R. & Bearhop, S. (2008) Applications of stable isotope analyses to avian ecology. *Ibis,* **150,** 447-461.

Ito, M., Takahashi, A., Kokubun, N., Kitaysky, A.S. & Watanuki, Y. (2010) Foraging behavior of incubating and chick-rearing thick-billed murres Uria lomvia. *Aquatic Biology,* **8,** 279-287.

Iverson, S.J., Springer, A.M. & Kitaysky, A.S. (2007) Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids. *Marine Ecology-Progress Series,* **352,** 235-244.

Kacelnik, A. (1984) Central Place Foraging in Starlings (Sturnus vulgaris). I. Patch Residence Time. *Journal of Animal Ecology,* **53,** 283-299.

Kitaysky, A.S., Piatt, J.F., Hatch, S.A., Kitaiskaia, E.V., Benowitz-Fredericks, Z.M., Shultz, M.T. & Wingfield, J.C. (2010) Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Functional Ecology,* **24,** 625-637.

Kitaysky, A.S., Piatt, J.F. & Wingfield, J.C. (2007) Stress hormones link food availability and population processes in seabirds. *Marine Ecology-Progress Series,* **352,** 245-258.

Kitaysky, A.S., Wingfield, J.C. & Piatt, J.F. (1999) Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. *Functional Ecology,* **13,** 577-584.

Klostermann, M.R., Scopel, L.C. & Drummond, B.A. (2011) Biological monitoring at St. George Island, Alaska in 2011. *AMNWR 2011/11.* U.S. Fish and Wildl. Serv. Rep., Homer, Alaska.

Lack, D. (1946) Competition for Food by Birds of Prey. *Journal of Animal Ecology,* **15,** 123-129.

Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D.J. (2000) WinBUGS - A Bayesian modelling framework: Concepts, structure, and extensibility. *Statistics and Computing,* **10,** 325-337.

Markman, S., Pinshow, B. & Wright, J. (1999) Orange-Tufted Sunbirds Do Not Feed Nectar to Their Chicks. *The Auk,* **116,** 257-259.

Martínez del Rio, C. & Carleton, S.A. (2012) How fast and how faithful: the dynamics of isotopic incorporation into animal tissues. *Journal of Mammalogy,* **93,** 353-359.

Masello, J.F., Mundry, R., Poisbleau, M., Demongin, L., Voigt, C.C., Wikelski, M. & Quillfeldt, P. (2010) Diving seabirds share foraging space and time within and among species. *Ecosphere,* **1,** art19.

Mitani, Y., Sato, K., Ito, S., Cameron, M.F., Siniff, D.B. & Naito, Y. (2003) A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intensity data: results from two lactating Weddell seals. *Polar Biology,* **26,** 311-317.

Monaghan, P., Uttley, J.D., Burns, M.D., Thaine, C. & Blackwood, J. (1989) The Relationship Between Food Supply, Reproductive Effort and Breeding Success in Arctic Terns Sterna paradisaea. *Journal of Animal Ecology,* **58,** 261-274.

Montevecchi, W.A., Birt-Friesen, V.L. & Cairns, D.K. (1992) Reproductive Energetics and Prey Harvest of Leach's Storm-Petrels in the Northwest Atlantic. *Ecology,* **73,** 823-832.

Navarro, J., Forero, M.G., Gonzalez-Solis, J., Igual, J.M., Becares, J. & Hobson, K.A. (2009) Foraging segregation between two closely related shearwaters breeding in sympatry. *Biology Letters,* **5,** 545-548.

Nystrom, K.G.K. & Pehrsson, O. (1988) Salinity as a constraint affecting food and habitat choice of mussel-feeding diving ducks. *Ibis,* **130,** 94-110.

Oelbermann, K. & Scheu, S. (2002) Stable isotope enrichment (delta N-15 and delta C-13) in a generalist predator (Pardosa lugubris, Araneae : Lycosidae): effects of prey quality. *Oecologia,* **130,** 337-344.

Orben, R.A., Irons, D.B., Shaffer, S.A. & Roby, D.D. (2012) Winter distribution and ecology of black-legged kittiwakes (*Rissa tridactyla*) and thick-billed murres (*Uria lomvia*) breeding at two Bering Sea colonies with differing population trends. (ed. p. North Pacific Research Board Final Report 911).

Parnell, A.C., Inger, R., Bearhop, S. & Jackson, A.L. (2010) Source partitioning using stable isotopes: Coping with too much variation. *Plos One,* **5,** doi:10.1371/journal.pone.0009672.

Pennycuick, C.J. (1987) Flight of auks (Alcidae) and other northern seabirds compared with southern procellariiformes - ornithodolite observations. *Journal of Experimental Biology,* **128,** 335-347.

Pianka, E.R. (1969) Sympatry of Desert Lizards (Ctenotus) in Western Australia. *Ecology,* **50,** 1012-1030.

Romero, L.M. & Reed, J.M. (2005) Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology,* **140,** 73-79.

Satterthwaite, W.H., Kitaysky, A.S. & Mangel, M. (2012) Linking climate variability, productivity and stress to demography in a long-lived seabird. *Marine Ecology-Progress Series,* **454,** 221-+.

Schoener, T.W. (1974) Resource Partitioning in Ecological Communities. *Science,* **185,** 27-39.

Semmens, B.X., Ward, E.J., Moore, J.W. & Darimont, C.T. (2009) Quantifying inter- and intra-population niche variability using hierarchical Bayesian stable isotope mixing models. *Plos One,* **4,** doi:10.1371/journal.pone.0006187.

Spear, L.B. & Ainley, D.G. (2007) Storm-Petrels of the Eastern Pacific Ocean: Species Assembly and Diversity along Marine Habitat Gradients. *Ornithological Monographs*, iii-77.

Takahashi, A., Matsumoto, K., Hunt Jr, G.L., Shultz, M.T., Kitaysky, A.S., Sato, K., Iida, K. & Watanuki, Y. (2008a) Thick-billed murres use different diving behaviors in mixed and stratified waters. *Deep Sea Research Part II: Topical Studies in Oceanography,* **55,** 1837-1845.

Takahashi, A., Matsumoto, K., Hunt Jr, G.L., Shultz, M.T., Kitaysky, A.S., Sato, K., Iida, K. & Watanuki, Y. (2008b) Thick-billed murres use different diving behaviors in mixed and stratified waters. *Deep Sea Research Part II: Topical Studies in Oceanography,* **55,** 1837-1845.

Thompson, D.R., Lilliendahl, K., Solmundsson, J., Furness, R.W., Waldron, S. & Phillips, R.A. (1999) Trophic relationships among six species of Icelandic seabirds as determined through stable isotope analysis. *Condor,* **101,** 898-903.

Tremblay, Y., Cherel, Y., Oremus, M., Tveraa, T. & Chastel, O. (2003) Unconventional ventral attachment of time–depth recorders as a new method for investigating time budget and diving behaviour of seabirds. *Journal of Experimental Biology,* **206,** 1929-1940.

Van Pelt, T.I., Piatt, J.F., Lance, B.K. & Roby, D.D. (1997) Proximate composition and energy density of some north pacific forage fishes. *Comparative Biochemistry and Physiology Part A: Physiology,* **118,** 1393-1398.

Weimerskirch, H. & Cherel, Y. (1998) Feeding ecology of short-tailed shearwaters: breeding in Tasmania and foraging in the Antarctic? *Marine Ecology Progress Series,* **167,** 261-274.

Whitman, L.D. (2010) Variation in the Energy Density of Forage Fishes and Invertebrates from the Southeastern Bering Sea. Master of Science, Oregon State University.

Williams, C.T., Buck, C.L., Sears, J. & Kitaysky, A.S. (2007) Effects of nutritional restriction on nitrogen and carbon stable isotopes in growing seabirds. *Oecologia,* **153,** 11-18.

Williams, C.T., Iverson, S.J. & Buck, C.L. (2008) Stable isotopes and fatty acid signatures reveal age- and stage-dependent foraging niches in tufted puffins. *Marine Ecology-Progress Series,* **363,** 287-298.

Wilson, R.P. (2010) Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Functional Ecology,* **24,** 646-657.

Wingfield, J.C., Vleck, C.M. & Moore, M.C. (1992) Seasonal-changes of the andrenocortical-response to stress in birds of the sonoran desert. *Journal of Experimental Zoology,* **264,** 419-428.

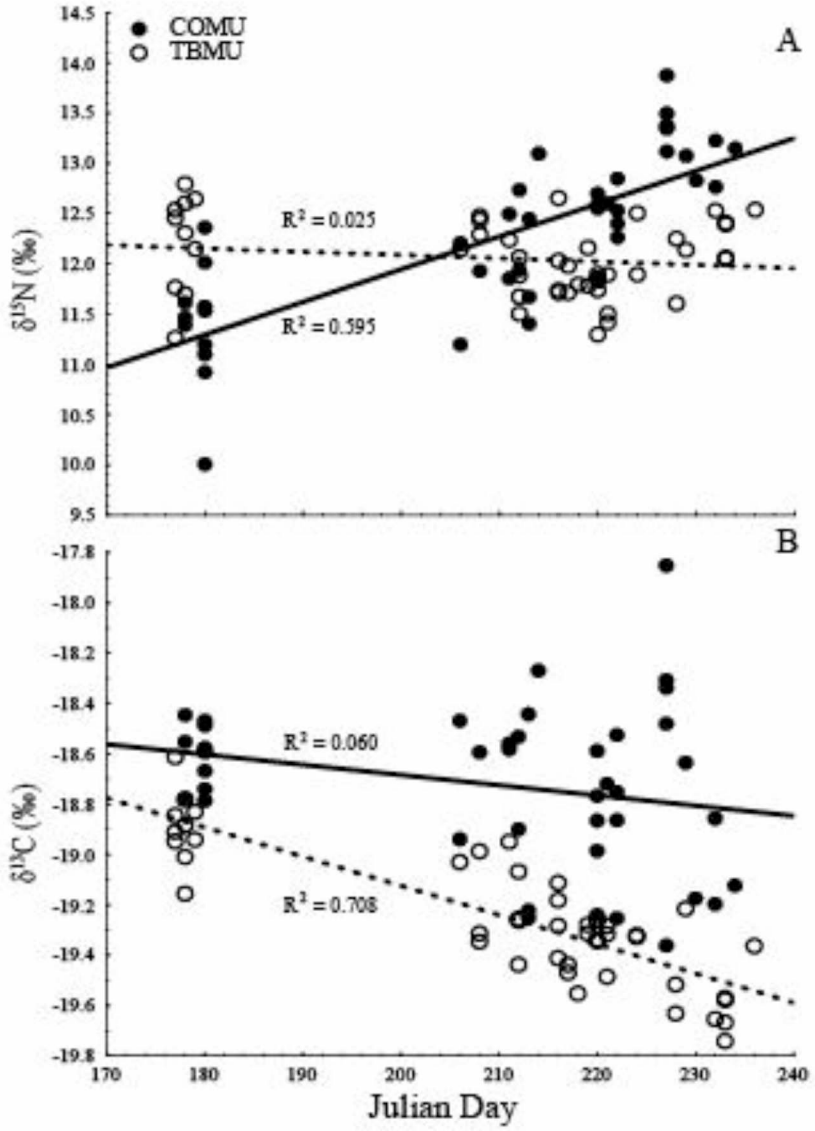

Figure 2.1. Stable isotope ratios of common and thick-billed murres. Seasonal changes in stable isotope signatures of adult common (filled circles) and thick-billed (open circles) murres breeding on Bogoslof I. in 2009: (*a*) $\delta^{15}N$ and (*b*) $\delta^{13}C$. Lines represent linear regressions (and associated R^2-values) for common (solid line) and thick-billed (dashed line) murres. Julian dates before 190 represent the incubation stage and thereafter the chick-rearing stage.

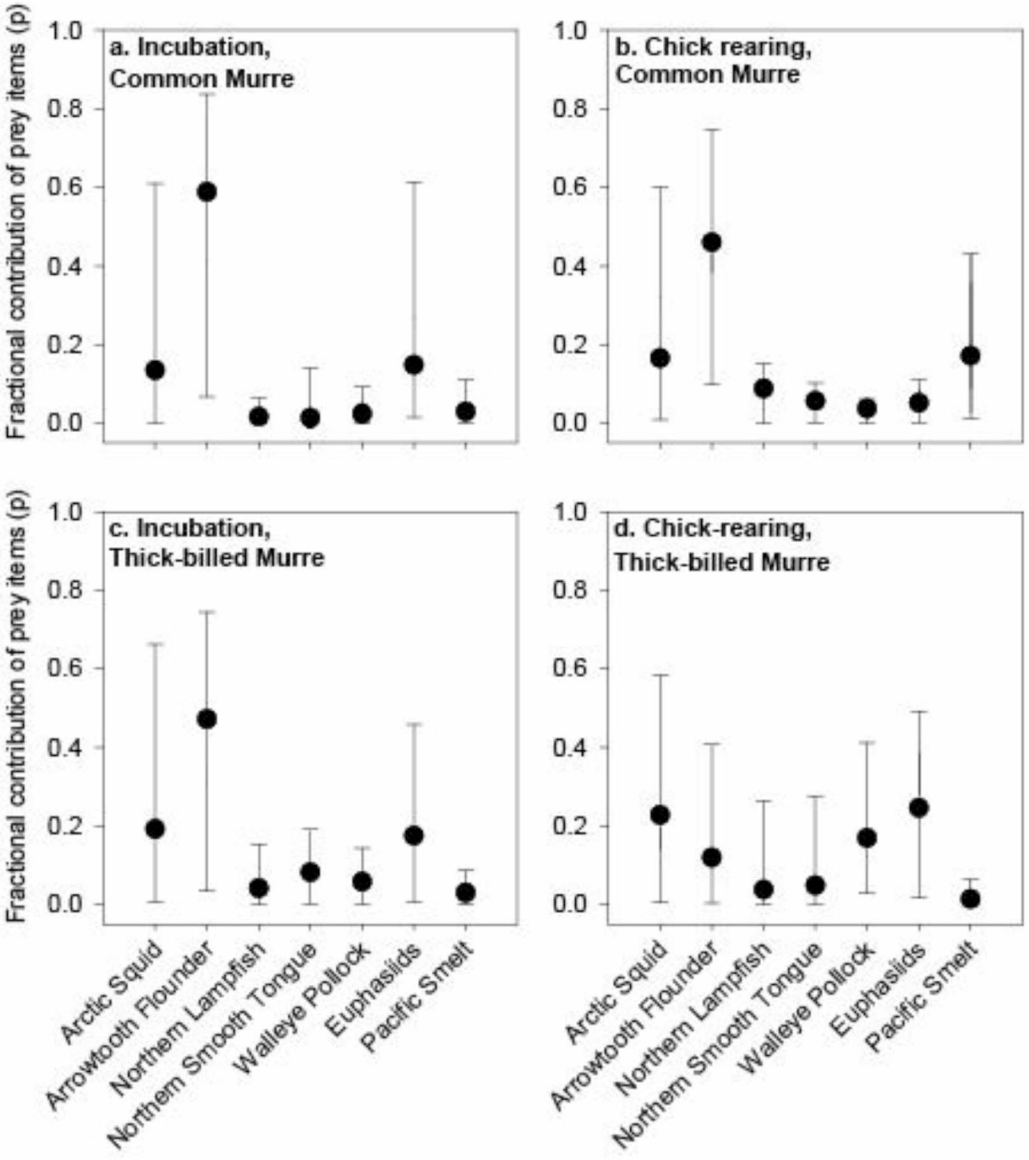

Figure 2.2. Diet compositions of incubating and chick-rearing common and thick-billed murres. Estimated by the Bayesian Mixing Analysis of stable isotope signatures of birds (red-blood cells) and those of their potential prey (whole body lean tissues). Figure shows posterior means and 95% credible intervals of the fractional contribution (p) of seven different prey species that were sampled in the vicinity of breeding colony in 2009.

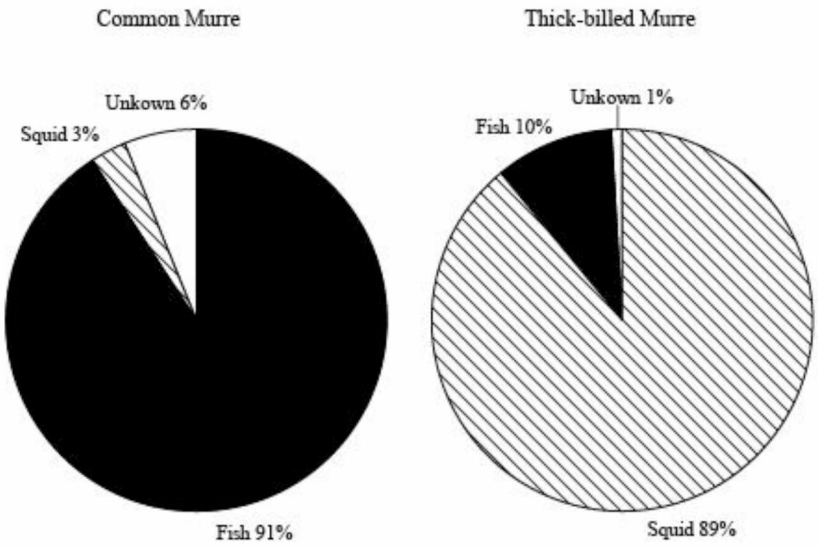

Figure 2.3. Diet compositions of common and thick-billed murre chicks (based on direct observations of prey delivered). Fish were the primary item (91%) in common murre chick diets compared to squid (89%) in thick-billed murre chick diets.

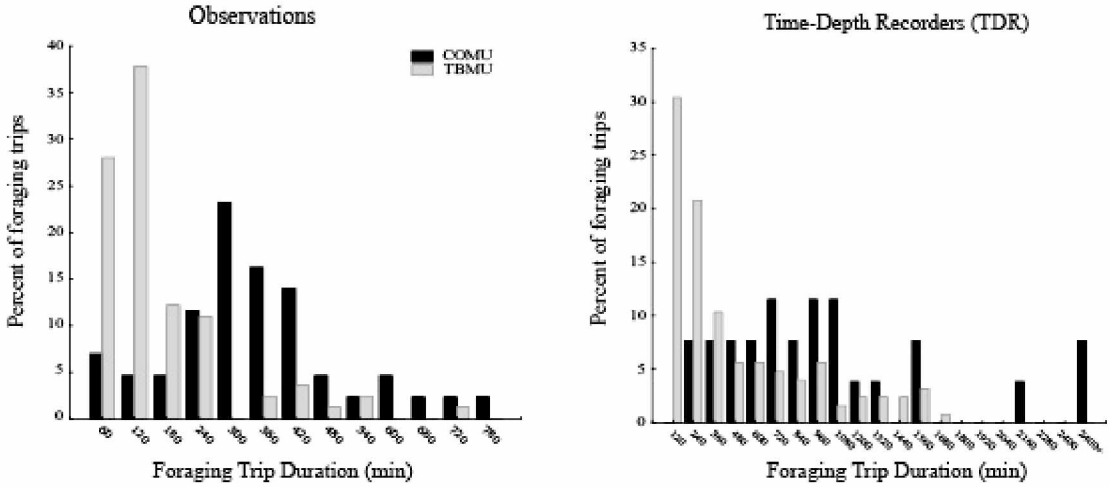

Figure 2.4. Foraging trip durations of common and thick-billed murres based on direct observations of individuals attending nest (left panel) and obtained with bird-born time-depth recorders (TDR, right panel). Results obtained by both techniques agreed that common murres (black bars) had longer foraging trips than thick-billed murres (gray bars). Direct observations of nests were limited to an 18 hr period of daylight and thus represent only trips completed during a period that was equal or shorter than 18 hrs. The use of TDR loggers allowed us to record longer (overnight) foraging trips performed by breeding birds.

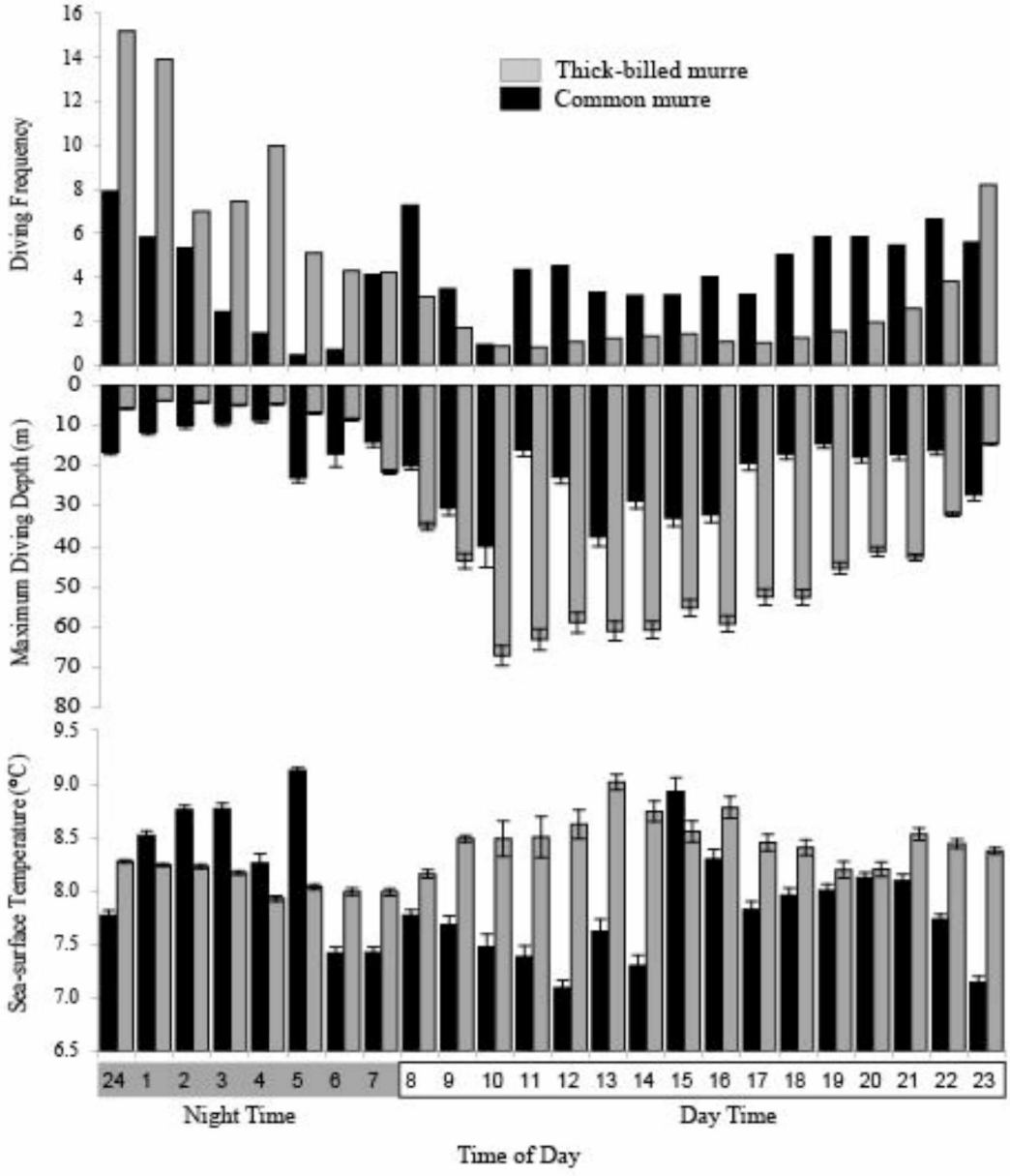

Figure 2.5. Temporal variation in foraging patterns of chick-rearing murres (assessed with the TDR bird-born data loggers). *Upper panel*: thick-billed (28 birds, 10,267 dives, gray bars) murres performed more of their foraging dives at night (2400 - 0659)

compared to common (11 birds, 5,282 dives, black bars) murres (each bar represents the mean proportion of dives per time window). *Middle panel*: when foraging at night, common murres targeted prey at deeper depths than thick-billed murres. Each bar represents the mean max depth per dive ± SE. *Low panel*: on average, common murres foraged in colder waters (e.g. lower SST) than thick-billed murres, except during the night hours when common murres foraged in warmer waters. Each bar represents the average max SST per foraging bout ± SE.

CHAPTER 3

MITOCHONDRIAL DNA VARIATION IN COMMON MURRES (*URIA AALGE*) BREEDING ON DECLINING, STABLE AND INCREASING COLONIES IN THE BERING SEA[1]

ABSTRACT

Recent studies suggest that different genotypes of long-lived birds might be differentially affected by changing environmental conditions. The aim of this study was to investigate the link between genetic diversity and population trajectories of long-lived seabirds (the common murre, *Uria aalge*) breeding at three colonies in the south-eastern Bering Sea. During the past four decades, murres breeding on these colonies have shown contrasting numerical trends: a strong 3-fold decline on St. Paul, relative stability on St. George and an increase on Bogoslof. During 1999-2009 at each colony, we non-lethally collected blood samples from a large number of chick-rearing adult murres. We compared colonies using mtDNA structure based on the NADH dehydrogenase subunit 2 (ND2) sequences. Similar to previous studies, our analyses revealed low levels of mtDNA variation and lack of geographic structuring in mtDNA variation (F_{st} and φ_{st} values), suggestive of high levels of gene flow among the colonies. We found significantly negative Tajima's D for both synonymous and non-synonymous sites among all the

[1]Barger, C. P., S. V. Drovetski, & A. S. Kitaysky. Mitochondrial DNA variation in common murres (*Uria aalge*) breeding on declining, stable and increasing colonies in the Bering Sea. Prepared for AUK.

colonies, indicating population size expansion (after a bottleneck or selective sweep) or purifying selection. Contrary to our expectations, *R2* (Ramos-Onsins and Rozas 2002) and F_S (Fu 1997) tests did not reflect contrasting population trajectories during the last 40 years between declining St. Paul and stable St. George and Bogoslof colonies. However, haplotype diversity (Hd) and non-synonymous nucleotide diversity (π_{NS}) were larger on Bogoslof (a stable/increasing colony) compared to St. Paul (a declining colony). We did not detect a difference in the nucleotide diversity (π_S) for synonymous sites, even though the ratio of π_{NS} / π_S was twice as large on Bogoslof (0.187) compared to St. Paul (0.081). We also found a significantly larger ratio of non-synonymous to synonymous individuals and haplotypes in the ND2 gene among birds breeding at Bogoslof as compared to those on St. Paul. We conclude that environmental variability and breeding conditions may contribute to low genetic diversity of the Pacific common murre at declining colonies.

Introduction

Population cycles are common in many vertebrate species, resulting in large population fluctuations (Krebs et al. 1995, Krebs 1996). In long-lived avian species, periodic removals of a significant proportion of individuals might affect micro-evolutionary processes and cause significant changes in genetic diversity (Drovetski et al. 2012; Reiertsen et al. 2012 and references therein), which could have important implications for conservation purposes. Among long-lived seabirds, the Pacific common murre *Uria aalge* (hereafter murre) provides an ideal system to study the effects of environmentally driven population cycles on micro-evolutionary processes. Murres are one of the most abundant fish-eating colonial seabirds in the North Pacific, with an estimated population size of 6 million (Ainley et al. 2002). Murres have a long life expectancy (~22-28 years (Clapp et al. 1982, Thomas E. Reed et al. 2008)), and slow reproductive rates (delayed sexual maturity (~3-5 years) and a single-egg clutch size). However, common murres in the North Pacific undergo periodic (~5-8 years) massive die-off events, typically occurring on the wintering grounds, and a single die-off event can remove as much as 9% of the entire population (Bailey & Davenport 1972, Piatt & VanPelt 1997, Drovetski et al. 2012). Selection during these periodic die-off events may explain the low levels of genetic diversity observed in the Pacific population of this species (Friesen et al. 1996, Morris-Pocock et al. 2008, Drovetski et al. 2012). Previously, we showed that periodic die-offs affect different genetic haplotypes in a non-random manner (Drovetski et al. 2012). Here we examine whether similar selection

processes might lead to the genetic structuring of colonies with contrasting numerical trends during the last four decades.

A recent study by Morris-Pocock et al. (2008) showed a lack of geographical structuring of common murres in the Pacific compared to their sister species, the thick-billed murre (*Uria lomvia*), using a combination of mtDNA, nuclear genes, and microsatellites (Friesen et al. 1996, Friesen & Piatt 2003, Morris-Pocock et al. 2008). A common pattern appears in the mtDNA structure of Pacific common murres: a single haplotype dominates and few single point mutations arise from this dominant haplotype. The resulting genetic diversity is much lower than that of the congeneric species (Drovetski et al. 2012). Drovetski et al. (2012) examined individuals from a most recent die-off, and found that individuals with any mutation on the NADH dehydrogenase subunit 2 (ND2) mitochondrial gene, a gene involved in ATP synthesis, die-off in disproportionately high numbers during these mortality events, which the authors considered as evidence of natural selection. During this massive die-off event, carriers of the dominant haplotype died at a relatively low frequency, while carriers of non-synonymous and synonymous mutations died at similarly higher frequencies. Even though synonymous mutations, in short coding regions, do not result in a direct amino acid substitution they have been shown in previous studies to be responsive to selective pressures in large populations (Akashi 1994, Comeron et al. 1999). Specifically, carriers of a dominant ND2 haplotype were less likely to be affected by a die-off event compared to carriers of either synonymous or non-synonymous mutations. However, it is currently

unclear if a similar process of selection is also occurring at colonies of murres that have experienced gradual changes in population size during the recent decades.

The numerical trajectories of seabirds breeding on the neighboring islands in the south-eastern Bering Sea have shown contrasting trends during the last 40 years (Renner & Williams 2005, Byrd et al. 2008, Klostermann et al. 2011, Thomson & Drummond 2011). During 1976-2011, common murres breeding on St. Paul I. have experienced a strong and continuous decline, whereas their numbers have been relatively stable or increasing on neighboring St. George and Bogoslof Islands. These contrasting numerical changes are thought to be driven by the climate variability differentially affecting availability of food resources to fish-eating seabirds breeding on these islands (Byrd et al. 2008, Satterthwaite et al. 2012). During reproduction, foraging success of this and other species depends on the availability of forage fish in the vicinity of breeding colonies (Iverson et al. 2007, Kitaysky et al. 2007, Satterthwaite et al. 2012), which is affected by changes in environmental conditions (Benowitz-Fredericks et al. 2008, Barger & Kitaysky 2012, Dorresteijn et al. 2012). Furthermore, food-related stress is one of the major factors affecting reproduction and survival of seabirds breeding in the northern Pacific and Bering Sea regions (Kitaysky et al. 2007, Satterthwaite et al. 2012). Prolonged periods of food shortages during reproduction may lead to numerical changes at a given colony via decreased survival and/or increased immigration (Satterthwaite et al. 2012). Thus, contrasting demographic trends among the colonies may be indicative of long-term sub-optimal foraging conditions at the colony level, and have the potential to

drive processes which shape the pattern of genetic diversity (Lerner et al. 2009, Karell et al. 2011).

A long-term study conducted on Atlantic populations of common murres (Reiertsen et al. 2012), provided strong empirical evidence that changing environmental conditions have opposite effects on the survival rates of two distinct genetic morphs. Reiertsen et al. (2012) have concluded that further warming in the North Atlantic may induce directional changes that will alter relative frequencies of the two morphs. Strong effects of environmental conditions on phenotype frequencies have also been found in other avian species (Galeotti et al. 2009, Karell et al. 2011). Galeotti et al. (2009) suggested that perturbations in the environment could alter the balance between gene frequencies, especially if the lifetime fitness of the different morphs was differentially affected by environmental changes.

In this study, we sampled a large number of individuals breeding on the three major colonies of Bogoslof, St. George and St. Paul islands in the south-eastern Bering Sea to determine if stronger selection is occurring on a declining colony compared to stable/increasing colonies. If purifying selection against carriers of different haplotypes operates, then we expected to find lower genetic diversity and lower ratio of non-synonymous to synonymous mutations among birds breeding at declining compared to stable/increasing colonies.

Methods

Study Sites, Species and Bird Sampling

During 1999-2009, we sampled adult birds breeding at three large colonies with contrasting numerical trends (Table 3.1) (Byrd et al. 2008, Hunt Jr et al. 2008). The Bogoslof I. colony (~40,000 breeding murres) is situated in the Eastern Aleutians (53°55′38″N 168°02′04″W) and appeared to be stable or increasing over the last decades (Renner & Williams 2005). The St. George I. colony is situated in the Pribilof Islands (56°36′04″N 169°37′36″W), is the largest of all three colonies (~200,000 breeding common murres), and has been relatively stable since mid-1970. The St. Paul I. colony of common murres is also situated in the Pribilof Islands (57°07′21″N 170°16′20″W) and is similar in size to Bogoslof I. (~40,000 breeding individuals), but has been steadily declining since 1970, with a population decrease of approximately 70% during the last decades (Renner & Williams 2005, Byrd et al. 2008, Klostermann et al. 2011, Thomson & Drummond 2011). These three colonies also represent major differences in oceanographic conditions in the south-eastern Bering Sea; Bogoslof is surrounded by a deep ocean basin, St. George is within foraging distance of the continental shelf-break, and St. Paul is located on the continental shelf system (Hunt Jr et al. 2008). These differences in oceanographic conditions have been suggested as causal mechanisms determining the contrasting demographic trends (Byrd et al. 2008, Reiertsen et al. 2012).

Birds were captured with telescopic noose poles at their nesting sites and blood samples were collected from the brachial vein (for details of bird capture and blood collection methods see Benowitz-Fredericks et al. (2008)). All birds were banded with US Fish and Wildlife metal bands and released. Blood samples were centrifuged to

separate plasma and red blood cells. Red blood cells were used for whole genomic DNA extraction and sequencing.

DNA Amplification and Analysis

For all individuals, we sequenced the complete mtDNA ND2 gene (1041 bp) which is comprised of one exon. Genomic DNA was extracted using a DNeasy Blood and Tissue Kit (QIAGEN, Valencia, CA, USA). For PCR fragment amplification we used TaqGold (Applied Biosystems, Carlsbad, CA, USA) and primers L5215: 5'-TATCGGGCCCATACCCCGAAAAT-3' (Hackett 1996) and H1064: 5'-CTTTGAAGGCCTTCGGTTTA-3' (Drovetski et al. 2004). The PCR profile included 2.5min preheating at 94°C and 35 cycles of 30s at 94°C, 30s at 57°C and 45s at 72°C. PCR cycles were followed by 10 min of extension at 72°C. The PCR fragments were sequenced directly on ABI-3100 or ABI-3730 sequencers using BigDye chemistry (Applied Biosystems, Carlsbad, CA, USA) and amplification primers.

Sequences were aligned automatically in Sequencher v4.8 (Gene Codes Corporation). The number of haplotypes for each colony, and the nature of mutation of the dominant haplotype (synonymous and non-synonymous mutations) were identified using DNAsp v5.10.01 (Librado & Rozas 2009). DNAsp was also used for calculating haplotype (Hd), conducting intraspecific neutrality/demographic history tests using coalescent simulations with 10,000 replicates: Tajima's D (Tajima 1989, Tajima 1996), Fu's Fs (Fu 1997), and R2 (Ramos-Onsins & Rozas 2002) tests. Arlequin 3.5 (Excoffier et al. 1992, Excoffier & Lischer 2010) was used to calculated pairwise F_{st} and φ_{st} values among colonies. Nucleotide diversity (π_{NS} and π_S), theta (θ_{NS} and θ_S) and Tajima's D

(separately for synonymous and non-synonymous segregating sites) were also calculated using the program SITES (Hey & Nielsen 2007). To perform a Mantel's test (Mantel 1967) for isolation by distance between the breeding colonies we used the free access program IBDWS (Jensen et al. 2005). Colony-specific phylogenies were constructed using median-joining algorithms in the program Network 4.610 (Bandelt et al. 1999). We used the program R (v.2.11.1, R Foundation for Statistical Computing) to construct and analyze generalized linear models (GLM) to test for differences in the number synonymous and non-synonymous individuals, haplotypes and segregating sites (Hornik 2012).

Results

We did not detect a signature of intragenic recombination at this locus with the four gametic types test. Pairwise F_{st} and φ_{st} values were not significantly different between the colonies with (p-values > 0.05). Non-significant F_{st} and φ_{st} values indicated excessive gene flow among the colonies similar to previous studies (Table 3.3). Mantel's test of isolation by distance showed no significant relationships between genetic and geographical distances among the colonies ($r^2 = 0.407$; $p = 0.164$), the three colonies are separated by relatively short distances (Bogoslof:St. George 310 km; Bogoslof:St. Paul 387 km; St. George:St. Paul 79 km).

DNAsp identified 31 unique haplotypes at Bogoslof, 28 haplotypes at St. George, and 23 haplotypes at St. Paul (Table 3.2). In all colonies, a single haplotype dominated, which was similar to the findings of Drovetski et al. (2012). This dominant haplotype is clearly evident in our haplotype networks, with single point mutations arising from this

haplotype (Figure 3.1). We found significantly higher ratio of carriers of non-synonymous to synonymous mutations (GLM, $p = 0.029$), and a trend towards a higher ratio of non-synonymous to synonymous segregating sites (GLM, $p = 0.073$) on Bogoslof (increasing) compared to St. Paul (declining).

The calculated Hd and nucleotide diversity values for St. George, a relatively stable colony, were consistently intermediate between those for Bogoslof and St. Paul (Table 3.2). As expected, synonymous segregating sites had higher nucleotide diversity than non-synonymous sites on all three colonies, and synonymous nucleotide diversity (π_S) is similar among the colonies (Table 3.2). Murres breeding on Bogoslof, had higher Hd (0. 603) and π_n diversity (0.00043) when compared to those observed at St. Paul (0.483 and 0.00019, respectively). The ratio of π_{NS}/π_S and θ_{NS}/θ_S were also at least twice as large on Bogoslof (0.187 and 0.457) compared to St. Paul (0.081 and 0.174).

We found significantly negative Tajima's D p-values for all segregating sites among the colonies, indicating purifying selection, recent population expansion, and/or selective sweep (Lerner et al. 2009). Fu's Fs, and *R2* test values for each colony were all highly significant (Table 3.2). Contrary to our expectations, *R2* (Ramos-Onsins and Rozas 2002) and F_S (Fu 1997) tests did not indicate contrasting population trajectories between St. Paul, which has experienced a continuous 3-fold decline during the last 40 years, and stable/increasing colonies of St. George and Bogoslof Islands.

Discussion

In this study we examined mtDNA diversity at the ND2 gene of common murres breeding on three Bering Sea colonies with contrasting numerical trajectories. The results raise the possibility that purifying selection processes might be operating on ND2 or another mtDNA gene linked to ND2 at a colony level, and are thus more evident in a declining colony. Specifically, Bogoslof (a stable/increasing colony) had a larger proportion of carriers of non-synonymous mutations, higher haplotype diversity (0.603), higher non-synonymous nucleotide diversity (0.00043), higher ratio of π_{NS}/π_S (0.187) and θ_{NS}/θ_S (0.457) compared to those at the declining St. Paul colony (0.483, 0.00019, 0.081, 0.174, respectively (Table 3.2)). However, we did not detect a difference in synonymous nucleotide diversity π_S among the colonies and all site-specific Tajima's D p-values were significantly negative indicating that scenarios of a rapid population expansion and linked selective sweep cannot be excluded.

The ecological causes for a massive die-off event and population declines at a colony scale share many similarities. Both die-off events and population declines are reflective of food shortages in the environment. However, there is at least one major driving difference between the two events that could explain the disparity between results of this study and those found by Drovetski et al. (2012). During a die-off event, tolerance to starvation may drive selection for the dominant haplotype (Drovetski 2012). In contrast, actively breeding individuals examined in this study were not starving, as reproduction and starvation are not compatible in income-breeding long-lived seabirds (Kitaysky et al. 2007; 2010). However, selection on metabolic efficiency may still be occurring via effects on reproduction and chick survival. It is important to consider that

the ND2 gene is involved in the synthesis and production of ATP via the construction and regulation of the electron transport chain (Tieleman et al. 2009). It is possible that any mutations to the ND2 gene or a gene linked to ND2 will adversely affect an individual's efficiency in ATP synthesis, raising metabolic costs for birds already facing challenging foraging conditions. A metabolic inefficiency of energy conversion could affect an individual's reproductive success and survival. Therefore, selection may be acting on the survival of individuals suffering from starvation during cyclic die-offs (Drovetski et al. 2012), while purifying selection (this study) is probably acting by differentially affecting reproduction or emigration of carriers of different ND2 haplotypes.

Historic records and monitoring during the last decades indicate frequent changes in numerical size of common murre colonies in the North Pacific (Ainley et al. 2002). For example, during the last two centuries the number of common murres nesting on the Farallon Islands of California decreased from $0.5 - 1.5 \times 10^6$ pairs in the early 1800s to near extirpation in the 1930s. By 1982 numbers rebounded to 51,000 pairs, but declined to 26,000 pairs in 1985. Large fluctuations in population size were also common during the last four decades in many other colonies across the North Pacific (Dragoo et al. 2001, Ainley et al. 2002, Van Pelt and Shultz 2002, Byrd et al. 2008). These fluctuations suggest possible large scale periodic movements of birds among colonies, which could explain the observed high rates of gene flow among populations. Although adult murres are known to be highly faithful to their breeding colonies, several studies have reported relatively high dispersal rates of young birds (Halley & Harris 1993, Harris et al. 1996, Ainley et al. 2002). Since juvenile murres do not return to a colony to reproduce for 3-7

years, it is plausible that inexperienced young may be preferentially recruiting into food-rich colonies (such as Bogoslof) compared to food-poor colonies (such as St. Paul), which would result in a purifying selection pattern we observed in this study.

There are several potential reasons that might explain why selection may be operating more strongly on birds breeding on St. Paul compared to St. George and Bogoslof colonies. St. Paul is located in the Pribilof domain shelf system which is strongly affected by inter-annual variations in foraging conditions (Byrd et al. 2008). Individuals attempting reproduction at this declining St. Paul colony are also faced with less diverse foraging habitats compared to those breeding on stable/increasing St. George and Bogoslof colonies (Harding et al. in press; Paredes et al. in press). The narrow range of foraging opportunities available to birds breeding on St. Paul might further exacerbate the negative impacts of environmental variability on their food supply compared to birds breeding on St. George and Bogoslof colonies. Thus, frequent food shortages during reproduction are expected at St. Paul I., which is a likely cause of a declining numerical trajectory of common murres at this colony (Byrd et al. 2008), and might contribute to reduced genetic diversity.

In conclusion, our results do not contradict the purifying selection hypothesis for common murres breeding at a declining colony in the Bering Sea. Currently, we are unsure of the specific mechanisms of purifying selection acting upon breeding individuals in this species; however, differential effects of environmental variability (e.g. food shortages) on different ND2 haplotypes is a potential cause. The majority of functional genes are under purifying selection and the negative Tajima's D for non-

synonymous sites provides evidence for purifying selection on this locus (Comeron et al. 1999, Bustamante et al. 2005, Lerner et al. 2009). However we also detected negative Tajima's D on synonymous sites therefore, we cannot disentangle the specific mechanisms of purifying selection, rapid population expansion after a bottleneck and/or linked selective sweep. Future studies focusing on foraging ecology and physiological responses of different ND2 haplotypes to environmental changes might help to clarify the nature of selective factors causing low genetic diversity and selection in the breeding populations of Pacific common murres. Differences in foraging ecology and physiology by the mitochondrial haplotype are currently under investigation and remain a focal point for our future work. This study lays the framework for future experimental and field studies to demonstrate that breeding murres are in fact responding adaptively to climate change through selection processes.

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Literature Cited

Ainley DG, Nettleship DN, R. CH, Storey AE (2002) Common Murre (*Uria aalge*). In: The Birds of North America Online (A Poole, Ed). Cornell Lab of Ornithology, Ithaca

Akashi H (1994) Synonymous codon usage in Drosophila melanogaster: natural selection and translational accuracy. Genetics 136:927-935

Bailey EP, Davenport GH (1972) Die-off of Common Murres on the Alaska Peninsula and Unimak Island. Condor 74:215-219

Bandelt HJ, Forster P, Rohl A (1999) Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16:37-48

Barger CP, Kitaysky AS (2012) Isotopic segregation between sympatric seabird species increases with nutritional stress. Biology Letters 8:442-445

Benowitz-Fredericks ZM, Shultz MT, Kitaysky AS (2008) Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. Deep Sea Research Part II: Topical Studies in Oceanography 55:1868-1876

Bustamante CD, Fledel-Alon A, Williamson S, Nielsen R, Todd Hubisz M, Glanowski S, Tanenbaum DM, White TJ, Sninsky JJ, Hernandez RD, Civello D, Adams MD, Cargill M, Clark AG (2005) Natural selection on protein-coding genes in the human genome. Nature 437:1153-1157

Byrd GV, Schmutz JA, Renner HM (2008) Contrasting population trends of piscivorous seabirds in the Pribilof Islands: A 30-year perspective. Deep Sea Research Part II: Topical Studies in Oceanography 55:1846-1855

Clapp RB, Klimkiewicz MK, Kennard JH (1982) Longevity records of North American birds: Gaviidae through Alcidae. Journal of Field Ornithology 53:81-124

Comeron JM, Kreitman M, Aguadé M (1999) Natural selection on synonymous sites is correlated with gene length and recombination in Drosophila. Genetics 151:239-249

Dorresteijn I, Kitaysky AS, Barger C, Benowitz-Fredericks ZM, Byrd GV, Shultz M, Young R (2012) Climate affects food availability to planktivorous least auklets *Aethia pusilla* through physical processes in the southeastern Bering Sea. Marine Ecology-Progress Series 454:207-220

Drovetski SV, Kitaysky AS, Mode NA, Zink RM, Iqbal U, Barger C (2012) mtDNA haplotypes differ in their probability of being eliminated by a mass die-off in an abundant seabird. Heredity 109:29-33

Drovetski SV, Zink RM, Fadeev IV, Nesterov EV, Koblik EA, Red'kin YA, Rohwer S (2004) Mitochondrial phylogeny of Locustella and related genera. Journal of Avian Biology 35:105-110

Excoffier L, Lischer HEL (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources 10:564-567

Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from the metric distances among DNA haplotypes - Application to human mitochondrial DNA restriction data. Genetics 131:479-491

Friesen VL, Montevecchi WA, Baker AJ, Barrett RT, Davidson WS (1996) Population differentiation and evolution in the common guillemot *Uria aalge*. Molecular Ecology 5:793-805

Friesen VL, Piatt JF (2003) A genetic study to aid in restoration of murres, guillemots and murrelets to the Gulf of Alaska. In: Exxon Valdez Oil Spill Restoration Project Final Report. Alaska Biological Sciences Center, USGS: Anchorage, Alaska.

Fu Y-X (1997) Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915-925

Galeotti P, Rubolini D, Sacchi R, Fasola M (2009) Global changes and animal phenotypic responses: melanin-based plumage redness of scops owls increased with temperature and rainfall during the last century. Biology Letters 5:532-534

Hackett SJ (1996) Molecular phylogenetics and biogeography of tanagers in the Genus Ramphocelus(Aves). Molecular Phylogenetics and Evolution 5:368-382

Halley DJ, Harris MP (1993) Intercolony movement and behaviour of immature Guillemots *Uria aalge*. Ibis 135:264-270

Harris MP, Wanless S, Barton TR (1996) Site use and fidelity in the Common Guillemot *Uria aalge*. Ibis 138:399-404

Hey J, Nielsen R (2007) Integration within the Felsenstein equation for improved Markov chain Monte Carlo methods in population genetics. Proceedings of the National Academy of Sciences 104:2785-2790

Hornik K (2012) The R FAQ. In:

Hunt Jr GL, Stabeno PJ, Strom S, Napp JM (2008) Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof Domain. Deep Sea Research Part II: Topical Studies in Oceanography 55:1919-1944

Iverson SJ, Springer AM, Kitaysky AS (2007) Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids. Marine Ecology-Progress Series 352:235-244

Jensen JL, Bohonak AJ, Kelley ST (2005) Isolation by distance, web service. BMC Genet 6

Karell P, Ahola K, Karstinen T, Valkama J, Brommer JE (2011) Climate change drives microevolution in a wild bird. Nat Commun 2

Kitaysky AS, Piatt JF, Wingfield JC (2007) Stress hormones link food availability and population processes in seabirds. Marine Ecology-Progress Series 352:245-258

Klostermann MR, Scopel LC, Drummond BA (2011) Biological monitoring at St. George Island, Alaska in 2011. In: AMNWR 2011/11. U.S. Fish and Wildl. Serv. Rep., Homer, Alaska

Krebs CJ (1996) Population cycles revisited. Journal of Mammalogy 77:8-24

Krebs CJ, Boutin S, Boonstra R, Sinclair ARE, Smith JNM, Dale MRT, Martin K, Turkington R (1995) Impact of food and predation on the snowshoe hare cycle. Science 269:1112-1115

Lerner HRL, Johnson JA, Lindsay AR, Kiff LF, Mindell DP (2009) It's not too late for the Harpy Eagle (*Harpia harpyja*): High levels of genetic diversity and differentiation can fuel conservation programs. PLoS ONE 4:e7336

Librado P, Rozas J (2009) DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. Bioinformatics 25:1451-1452

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Research 27:209-220

Morris-Pocock JA, Taylor SA, Birt TP, Damus M, Piatt JF, Warheit KI, Friesen VL (2008) Population genetic structure in Atlantic and Pacific Ocean common murres (*Uria aalge*): natural replicate tests of post-Pleistocene evolution. Molecular Ecology 17:4859-4873

Piatt JF, VanPelt TI (1997) Mass-mortality of guillemots (*Uria aalge*) in the Gulf of Alaska in 1993. Mar Pollut Bull 34:656-662

Ramos-Onsins SE, Rozas J (2002) Statistical properties of new neutrality tests against population growth. Molecular Biology and Evolution 19:2092-2100

Reiertsen TK, Erikstad KE, Barrett RT, Sandvik H, Yoccoz NG (2012) Climate fluctuations and differential survival of bridled and non-bridled common guillemots *Uria aalge*. Ecosphere 3:art52

Renner HM, Williams JC (2005) Marine bird surveys at Bogoslof Island, Alaska, in 2005. In: AMNWR 2005/18. U.S. Fish and Wildl. Serv. Rep., Homer, Alaska

Satterthwaite WH, Kitaysky AS, Mangel M (2012) Linking climate variability, productivity and stress to demography in a long-lived seabird. Marine Ecology-Progress Series 454:221-+

Tajima F (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585-595

Tajima F (1996) The amount of DNA polymorphism maintained in a finite population when the neutral mutation rate varies among sites. Genetics 143:1457-1465

Thomas E. Reed, Loeske E. B. Kruuk, Sarah Wanless, Morten Frederiksen, Emma J. A. Cunningham, Michael P. Harris (2008) Reproductive senescence in a long lived seabird: Rates of decline in late life performance are associated with varying costs of early reproduction. The American Naturalist 171:E89-E101

Thomson G, Drummond BA (2011) Biological monitoring at St. Paul Island, Alaska in 2011. In: AMNWR 2011/11. U.S. Fish and Wildl. Serv. Rep., Homer, Alaska

Tieleman BI, Versteegh MA, Fries A, Helm B, Dingemanse NJ, Gibbs HL, Williams JB (2009) Genetic modulation of energy metabolism in birds through mitochondrial function. Proc R Soc B-Biol Sci 276:1685-1693

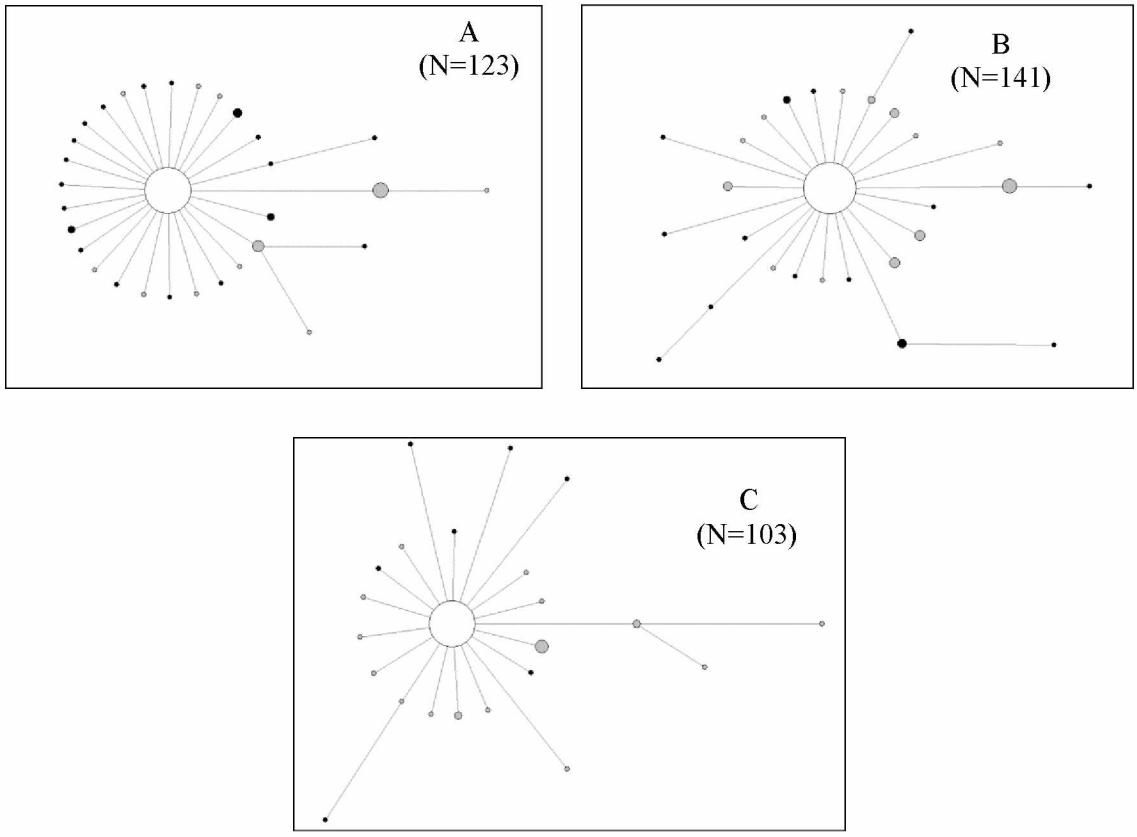

Figure 3.1. Median-joining haplotype network depicting relationships among ND2 haplotypes in common murres breeding on three Bering Sea colonies with contrasting population trajectories during the last decades: (A) Bogoslof (stable/increasing); (B) St George (stable), and (C) St. Paul (declining). Black circles represent non-synonymous substitutions, grey circles represent synonymous substitutions and white circles represent the dominant haplotype. Circle size is proportional to the number of individuals with that specific haplotype.

Table 3.1. Sampling years, locations, and sample sizes for analyses of mtDNA genetic structure of common murres breeding in the south-eastern Bering Sea.

Colony	Year	# individuals sampled for ND2 analyses
Bogoslof	1999	15
	2000	8
	2002	15
	2004	10
	2005	11
	2008	29
	2009	35
St. George	1999	10
	2000	15
	2003	22
	2004	23
	2005	18
	2008	18
	2009	35
St. Paul	2000	11
	2003	20
	2004	25
	2005	8
	2008	20
	2009	19

Table 3.2. Summary statistics of sample sizes, haplotype frequencies, genetic diversity and neutrality test statistics for common murres. "N dominant" is the number of individuals with the most common ND2 haplotype, "N non-synonymous" is the number of individuals whose ND2 haplotype differs from the most common haplotype by at least one non-synonymous mutation, "N synonymous" is the number of individuals whose ND2 haplotype differs from the most common haplotype by at least one synonymous mutation. "Number of synonymous haplotypes" and "Number of non-synonymous haplotypes" refers to the number of synonymous and non-synonymous haplotypes observed at each colony. "N haplotypes" refers to the number of unique haplotypes for a specific colony. Nucleotide diversity (π), Theta (θ) and Tajima's D were also calculated by site specifically and p-values for Tajima's D were estimated through coalescent simulations with 10,000 replicates.

Parameters	All Colonies	Bogoslof	St George	St Paul
N complete ND2	367	123	141	103
N dominant individuals	245	77	94	74
N synonymous individuals	74	23	29	22
N non-synonymous individuals	48	23	18	7
Number of synonymous haplotypes		11	13	15
Number of non-synonymous haplotypes		19	14	7
Number of Haplotypes		31	28	23
Hd		0.603	0.561	0.483
s.d.		0.053	0.051	0.062
Nucleotide diversity (π)		0.00091	0.00095	0.00077
s.d.		0.00011	0.00012	0.00014
Synonymous nucleotide diversity per site (π_S)		0.00232	0.00259	0.00236
Non-synonymous nucleotide diversity per site (π_{NS})		0.00043	0.00040	0.00019
Synonymous θ_S per site		0.00934	0.01192	0.01413
Non-synonymous θ_{NS} per site		0.00427	0.00393	0.00245
Tajima's D synonymous per site		-1.9677	-2.115	-2.3844
P-value		0.00300	0	0
Tajima's D non-synonymous per site		-2.4954	-2.4355	-2.3844
P-value		0	0	0
Fu's Fs	-139.018	-44.997	-35.128	-29.82
P-value	0	0	0	0
R2	0.0067	0.0156	0.0162	0.0196
P-value	0	0	0.005	0.0102

Table 3.3. Matrix of pairwise F_{ST} (above diagonal) and Φ_{ST} (below diagonal) comparisons of mtDNA ND2 among colonies.

	Bogoslof	St. George	St Paul
Bogoslof	---	-0.0013	0.006
St George	0.0009	---	0.00216
St Paul	0.0006	0.0018	---

CONCLUSIONS

In this study, we examined the circumstances and mechanisms of resource partitioning in two sympatric species of murre during incubation and chick-rearing stages. We also investigated the mtDNA structure of common murres breeding on three colonies with contrasting population trends and foraging conditions.

We found that inter-specific resource partitioning was influenced by environmentally driven changes in prey availability, and predictable increases in energy demands between the life-history stages. Specifically, in Chapter 1, we found that when food resources were limited during the incubation stage (as reflected in CORT), there was a significant increase in isotopic distance between the species, indicative of food resource partitioning. We also found evidence that environmental change affects the extent of resource partitioning: as water temperatures rise, common and thick-billed murres diverge in their diet composition and foraging locations. Predicted future warming of the oceanic regions of south-eastern Bering Sea is likely to interfere with successful reproduction of seabirds (Satterthwaite *et al.*, 2012), and the range of environmental conditions that murre species can tolerate by avoiding inter-specific competition for limited food resources remains to be examined.

In chapter 2, we found evidence for inter-specific resource partitioning during the transition from incubation to chick-rearing, which is associated with a predictable increase of energy expenditure in breeding seabirds. We did not observe changes in nutritional stress levels between incubation and chick-rearing in common or thick-billed

murre parents: levels of corticosterone were relatively low during the entire breeding season in both species. SI ratios suggest that inter-specific difference in diets were minor during incubation. However, during chick-rearing, adult murres partitioned food resources spatially (used different water masses for foraging), temporally (exhibited different diving patterns in relation to time of day, and foraging trip durations) and a shift in prey composition (differed in SI signatures of adult blood and prey composition of chick diets). Common murre chicks received a diet containing mostly pacific smelt (91%) compared to thick-billed murre chicks which where fed arctic squid (89%). Modeling of adult diets detected substantial differences between the species during chick-rearing: common murres foraged primarily on Arctic Squid, Arrowtooth Flounder and Pacific Smelt, while thick-billed murres foraged on Arctic Squid, Walleye Pollock and euphasiids. Many previous studies of adult murre diets have focused solely on chick deliveries (Barrett, Bakken & Krasnov, 1997, Birkhead & Nettleship, 1987). Our study suggests that adult diets cannot be inferred only from prey delivered by adult murres to their chicks.

We also observed a large inter-specific difference in foraging trip duration and flight distance of chick-rearing individuals. Common murres had significantly longer foraging trips, fewer prey deliveries and longer flight distances during chick-rearing when compared to thick-billed murres. This vast difference between the morphologically and ecologically similar species is a surprising result, as the optimal foraging theory predicts that if food is not limited (which was the case in our study) then both species would be foraging at similar distances from the breeding colony. One possible

explanation of this unexpected result is that parent common and thick-billed murres were using different strategies to maximize energy delivery to their young. Marine fish and invertebrates differ in their salt content: squid contain more salt (iso-osmotic to their environment) than fish (hypo-osmotic) (Hodum & Hobson, 2000). Arctic squid was the main prey item delivered to thick-billed chicks, thus, they had to excrete excess salt, which is an energy-demanding physiological process (Hedeholm, Grønkjær & Rysgaard, 2011, Nystrom & Pehrsson, 1988, Hodum *et al.*, 2000, Dosch, 1997). This could substantially reduce the usable energy contained in a prey item delivered by thick-billed murres. This provisioning strategy would require frequent delivery of low usable energy prey by adult thick-billed murres, which they could achieve by foraging in the immediate proximity of the colony and delivering food often. On the other hand, schooling fish were the primary prey of common murre chicks; which allowed common murre parents to deliver high usable energy prey less frequently. Another possible explanation is an adaptive specialization by adults. Common murres might be more efficient at capturing pelagic schooling fish (i.e. *Osmeridae* species in this study), whereas thick-billed murres are better suited for capturing a larger variety of prey including invertebrates (Birkhead *et al.*, 1987). These putative foraging specializations of common and thick-billed murres could contribute to their selection of different prey during a period of increased energy demands.

Lastly, in chapter 3 we examined mtDNA diversity at the ND2 gene of common murres breeding on three major colonies in the Bering Sea. We found higher genetic diversity on Bogoslof (increasing population size) compared to St. Paul (declining

population size). However, we also detected significantly negative Tajima's D values for both synonymous and non-synonymous segregating sites. This is indicative of rapid population expansion after a bottleneck, selective sweep and/or purifying selection. Currently, we cannot disentangle these specific mechanisms causing the observed low genetic diversity of common murres breeding at a declining colony. The mtDNA gene ND2 codes for a protein that is responsible for construction and regulation of the electron transport chain and base-pair substitutions in this coding region may have detrimental effects on metabolic pathways (Tieleman, Versteegh, Fries *et al.*, 2009) and put carriers of mutations on ND2 gene at a disadvantage. Our results do not contradict the hypothesis of purifying selection, and it is possible that either relaxed purifying selection on the increasing colony or strong purifying selection on the declining colony determined the observed pattern of genetic diversity.

Results of this study have shown that the implementation of varying physiological and molecular approaches might be useful to wildlife practitioners managing bird resources. Future studies concerning effects of warming climate on seabird populations in the sub-Arctic regions should investigate a range of environmental conditions that seabirds may tolerate by avoiding inter-specific competition via partitioning of food resources. For example, we found that under the current environmental conditions murres are employing this strategy, which might allow them to at least partially buffer themselves from consequences of food shortages. However, we examined the inter-specific interactions between species breeding at a colony with overall favorable foraging conditions. Whether similar results would be observed at food-limited colonies and under

extreme change in environmental conditions remain to be tested. Future studies might also expand the analysis of inter-colony differences in the genetic diversity by including other genes coding for metabolic pathways. Our results suggest that low genetic diversity of ND2 might be used as an indicator of population declines of common murre colonies with unknown histories. It is important to determine whether other mtDNA loci coding for metabolic pathways would show similar patterns observed in this study.

We conclude that results of this study provide novel insights into how seabirds respond to changing environmental conditions, which might help wildlife practitioners more effectively address current conservation issues concerning seabirds.

Literature Cited

Barrett, R.T., Bakken, V. & Krasnov, J.V. (1997) The diets of common and Brünnich's guillemots Uria aalge and U. lomvia in the Barents Sea region. *Polar Research* **16**, 73-84.

Birkhead, T.R. & Nettleship, D.N. (1987) Ecological relationships between Common Murres, Uria aalge, and Thick-billed Murres, Uria lomvia, at the Gannet Islands, Labrador. III. Feeding ecology of the young. *Canadian Journal of Zoology* **65**, 1638-1649.

Byrd, G.V., Schmutz, J.A. & Renner, H.M. (2008) Contrasting population trends of piscivorous seabirds in the Pribilof Islands: A 30-year perspective. *Deep Sea Research Part II: Topical Studies in Oceanography* **55**, 1846-1855.

Cherel, Y., Le Corre, M., Jaquemet, S., Menard, F., Richard, P. & Weimerskirch, H. (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. *Marine Ecology-Progress Series* **366**, 281-291.

Deagle, B.E., Gales, N.J. & Hindell, M.A. (2008) Variability in foraging behaviour of chick-rearing macaroni penguins Eudyptes chrysolophus and its relation to diet. *Marine Ecology-Progress Series* **359**, 295-309.

Doody, L.M., Wilhelm, S.I., Mckay, D.W., Walsh, C.J. & Storey, A.E. (2008) The effects of variable foraging conditions on common murre (Uria aalge) corticosterone concentrations and parental provisioning. *Hormones and Behavior* **53**, 140-148.

Dorresteijn, I., Kitaysky, A.S., Barger, C., Benowitz-Fredericks, Z.M., Byrd, G.V., Shultz, M. & Young, R. (2012) Climate affects food availability to planktivorous least auklets Aethia pusilla through physical processes in the southeastern Bering Sea. *Marine Ecology-Progress Series* **454**, 207-220.

Dosch, J.J. (1997) Salt tolerance of nestling laughing gulls: An experimental field investigation. *Colonial Waterbirds* **20**, 449-457.

Drovetski, S.V., Kitaysky, A.S., Mode, N.A., Zink, R.M., Iqbal, U. & Barger, C. (2012) mtDNA haplotypes differ in their probability of being eliminated by a mass die-off in an abundant seabird. *Heredity* **109**, 29-33.

Forero, M.G., Bortolotti, G.R., Hobson, K.A., Donazar, J.A., Bertelloti, M. & Blanco, G. (2004) High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. *Journal of Animal Ecology* **73**, 789-801.

Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific competition in natural communities - A review of field experiments with plants. *American Naturalist* **139**, 771-801.

Hedeholm, R., Grønkjær, P. & Rysgaard, S. (2011) Energy content and fecundity of capelin (<i>Mallotus villosus</i>) along a 1,500-km latitudinal gradient. *Marine Biology* **158**, 1319-1330.

Hodum, P.J. & Hobson, K.A. (2000) Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope (delta N-15 and delta C-13) analyses. *Marine Ecology-Progress Series* **198**, 273-281.

Inger, R. & Bearhop, S. (2008) Applications of stable isotope analyses to avian ecology. *Ibis* **150**, 447-461.

Ito, M., Takahashi, A., Kokubun, N., Kitaysky, A.S. & Watanuki, Y. (2010) Foraging behavior of incubating and chick-rearing thick-billed murres Uria lomvia. *Aquatic Biology* **8**, 279-287.

Kitaysky, A.S., Piatt, J.F., Hatch, S.A., Kitaiskaia, E.V., Benowitz-Fredericks, Z.M., Shultz, M.T. & Wingfield, J.C. (2010) Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Functional Ecology* **24**, 625-637.

Kitaysky, A.S., Piatt, J.F. & Wingfield, J.C. (2007) Stress hormones link food availability and population processes in seabirds. *Marine Ecology-Progress Series* **352**, 245-258.

Kitaysky, A.S., Wingfield, J.C. & Piatt, J.F. (1999) Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. *Functional Ecology* **13**, 577-584.

Klostermann, M.R., Scopel, L.C. & Drummond, B.A. (2011) Biological monitoring at St. George Island, Alaska in 2011. *AMNWR 2011/11*. U.S. Fish and Wildl. Serv. Rep., Homer, Alaska.

Lack, D. (1946) Competition for Food by Birds of Prey. *Journal of Animal Ecology* **15**, 123-129.

Monaghan, P., Uttley, J.D., Burns, M.D., Thaine, C. & Blackwood, J. (1989) The Relationship Between Food Supply, Reproductive Effort and Breeding Success in Arctic Terns Sterna paradisaea. *Journal of Animal Ecology* **58**, 261-274.

Montevecchi, W.A., Birt-Friesen, V.L. & Cairns, D.K. (1992) Reproductive Energetics and Prey Harvest of Leach's Storm-Petrels in the Northwest Atlantic. *Ecology* **73**, 823-832.

Navarro, J., Forero, M.G., Gonzalez-Solis, J., Igual, J.M., Becares, J. & Hobson, K.A. (2009) Foraging segregation between two closely related shearwaters breeding in sympatry. *Biology Letters* **5**, 545-548.

Nystrom, K.G.K. & Pehrsson, O. (1988) Salinity as a constraint affecting food and habitat choice of mussel-feeding diving ducks. *Ibis* **130**, 94-110.

Pianka, E.R. (1969) Sympatry of Desert Lizards (Ctenotus) in Western Australia. *Ecology* **50**, 1012-1030.

Piatt, J.F. & Vanpelt, T.I. (1997) Mass-mortality of guillemots (Uria aalge) in the Gulf of Alaska in 1993. *Marine Pollution Bulletin* **34**, 656-662.

Renner, H.M. & Williams, J.C. (2005) Marine bird surveys at Bogoslof Island, Alaska, in 2005. *AMNWR 2005/18*. U.S. Fish and Wildl. Serv. Rep., Homer, Alaska.

Satterthwaite, W.H., Kitaysky, A.S. & Mangel, M. (2012) Linking climate variability, productivity and stress to demography in a long-lived seabird. *Marine Ecology-Progress Series* **454**, 221-+.

Schoener, T.W. (1974) Resource Partitioning in Ecological Communities. *Science* **185**, 27-39.

Thompson, D.R., Lilliendahl, K., Solmundsson, J., Furness, R.W., Waldron, S. & Phillips, R.A. (1999) Trophic relationships among six species of Icelandic seabirds as determined through stable isotope analysis. *Condor* **101**, 898-903.

Tieleman, B.I., Versteegh, M.A., Fries, A., Helm, B., Dingemanse, N.J., Gibbs, H.L. & Williams, J.B. (2009) Genetic modulation of energy metabolism in birds through mitochondrial function. *Proceedings of the Royal Society B-Biological Sciences* **276**, 1685-1693.

Weimerskirch, H., Jouventin, P. & Stahl, J.C. (1986) Comparative ecology of the 6 albatross species breeding on the crozet islands. *Ibis* **128**, 195-213.

Wilson, R.P. (2010) Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Functional Ecology* **24**, 646-657.

Wingfield, J.C., Vleck, C.M. & Moore, M.C. (1992) Seasonal-changes of the andrenocortical-response to stress in birds of the sonoran desert. *Journal of Experimental Zoology* **264**, 419-428.